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Age structure and dynamics in stands of bilberry
(*Vaccinium myrtillus* L.)

Ålder, struktur och dynamik hos blåbärsbestånd

by

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STOCKHOLM

Preface

The investigation reported here developed from a suggestion made in 1965 by Professor C. O. Tamm that I should study regeneration and growth in Vaccinium myrtillus — bilberry.

Preliminary studies suggested that the vegetative growth of this species involved interesting problems of spatial variation in several morphological features, for which an explanation was sought. A possible cause of these was suggested by Watt's concept of the relationship between the age and vigour of a perennial plant; and subsequently by the application of this concept to another dwarf shrub, Calluna vulgaris. Dwarf shrubs are a widespread and frequently dominant component of the field layer vegetation, not only in forest stands but also in heathlands, arctic and alpine tundra, not least in northern Eurasia. Many of them, in particular the North American Vaccinium species, form markedly clonal stands; and not a few are of commercial importance, wild or domesticated. For many animals their leaves, shoots and fruits are a valuable source of food.

Yet surprisingly little is known about the structure and dynamics of dwarf shrubs, with the possible exception of Calluna in semi-natural or managed stands. Structure here implies age structure, since age is the determining factor underlying much of the spatial variation in stands formed by the vegetative expansion of individual plants. Since the study of aggregates of such stands presents considerable difficulty, here isolated bilberry stands have been studied, in the expectation that a basic unit can be distinguished. This study is confined to the investigation of the age structure of such stands, and to its relation to spatial variation in standing crop, production and performance. An attempt is made to discover a character suitable as a basis for comparison of stands, ultimately with the aim of proceeding to the study of interactions, with both the physical environment and other plants.

Acknowledgements

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During the work in Scotland, Professor Charles Gimingham gave advice and encouragement which were much appreciated. The courtesy of His Grace the Duke of Fife made access to the site Cammachmore possible. His Factor kindly arranged to preserve part of the area for future study.

Without such cooperation from landowners, much fieldwork would be impossible.

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Any errors are of course my own.

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J. G. K. Flower-Ellis

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Abstract

Population age structure and dynamics were studied in isolated bilberry (*Vaccinium myrtillus* L.) stands on mainly two forest site types in Middle Sweden. Stands expand centrifugally by rhizome growth. Primary rhizomes decay, releasing branches, to form successive generations of units bearing tillers distally. The senior tillers on each unit mingle with younger tillers on succeeding units which overlap their predecessor; the oldest tillers are in the middle of the rhizome unit. In the clonal hierarchy of tillers which results, the basal area of the five largest stems, quadrat standing crop and yield are related to the age of the oldest tiller on the quadrat. Rhizome weight is related to the age of the oldest rhizome. Tiller longevity, mortality rate and standing dead differed between sites and stands studied; ingrowth into the population in densely stocked stands may be dependent on death of senior tillers. An empirical model was constructed for weight increment of aerial axes, based on shoot weight—length—age relationships. The pattern of litter fall in the stand was inferred. The suitability of characters studied in stand comparisons is discussed; individual or areal basal area increment of the dominant tillers was considered most useful.

Definitions

<u>Stand</u>	the aboveground part of the bilberry plant as a whole, consisting of aerial shoots derived from the orthotropic shoots which result from the adoption of an ageotropic posture by rhizome apices; recognisable in the field as a vegetation patch.
<u>Rhizome unit</u>	a branched system of rhizomes of various orders which bear aerial shoots distally, the age of which increases towards the older, proximal, end of the rhizome which is limited by decay or insect damage.
<u>Tiller</u>	the aboveground shoot developed from the orthotropic shoot; the "individual" of population studies.
<u>Aerial shoot</u>	a general term for the aboveground part of the plant, used interchangeably with "tiller".
<u>Axis</u>	a system of annual shoot increments formed by the branching of the original aerial shoot or subsequently, by the branching of a shoot arising from the lower part of this; of limited longevity.
<u>Bush</u>	an entity consisting of axes of various ages, some of which are living and others, dead.
<u>Long shoot</u>	any current shoot which is not less than one-third of the length of the longest shoot in a quadrat population of current shoots; used as equivalent to "vegetative shoot" but including some flowering shoots.
<u>Short shoot</u>	any current shoot shorter than the above limit; used as equivalent to "flowering shoot" but including some short vegetative shoots.
<u>Flowering shoot</u>	any short shoot having a short spur below the lowermost leaf, denoting the former presence of a flower.
<u>Current shoot</u>	the shoot formed in the year of sampling, abbreviated C. Older shoots are counted backwards from this, viz. C+1, C+2, etc.
<u>TS</u>	transverse section of stem on which annual rings are counted.
<u>Stem</u>	the lowermost part of the aboveground shoot.

Various definitions relating to sampling techniques may be found in the relevant places in the text, or in the Appendix.

Introduction

The investigation reported here deals with the structure, growth and dynamics of isolated stands of bilberry (*Vaccinium myrtillus* L.), mainly on two forest site types in middle Sweden.

Bilberry is a deciduous dwarf shrub with an extensive rhizome system. The aerial shoots are usually between 10-60 cm in height, initially assimilating, markedly angular and bear alternate, ovate leaves with a serrulate margin and an acute (though occasionally obtuse) apex. The stem base is terete. Aerial shoots die back from the tip when old and tend to become prostrate, giving the bush a hollow, straggling appearance. New shoots arise from the lower part of older axes or from the stem base itself, but tillers are derived primarily from orthotropic shoots or from buds on the rhizome axis (cf. *V. angustifolium* : Barker & Collins 1963).

Studies made in the Soviet Union on the structure of bilberry populations indicate that the bush expands by the development of shoots from dormant basal buds, while the original axis continues its growth (Zlobin 1961). In time this withers, leaving peripheral shoots to continue their growth (see Fig. 1). Eventually, these too wither, leaving a few small, leafy shoots at their base. The lifespan of the aerial axis varies considerably; Zlobin gives 12 years as the maximum age attained by axes in the spruce forest in which he made his studies, but elsewhere the lifespan may be much less. The bush may attain an age of some 20 years, according to Zlobin, but other workers, e.g. Keso (1908), Ritchie (1955b), Kanngiesser (1909, 1914) give ages nearer 30 years, for material from Finland, from moorland near Sheffield (England) and from high-lying sites in Central Europe, respectively.

The axis consists of two structural elements: long, or vegetative shoots, which generally persist to form the main framework of the bush, and short, predominantly flowering shoots, which normally have a solitary flower in the axil of the lowermost leaf or rarely, a second flower in the axil of the leaf above. Such shoots after fruiting often fall with the leaves in autumn or during the winter (Grevillius & Kirchner 1923).

On a single bush there may be much variation, not only in the length of the shoots formed in any year, but also in the size of the leaves. The uppermost shoots tend to be short and small-leaved (Lindman 1914); see Fig. 2. This may depend partly on the predominance of flowering shoots in the upper part of each axis. On axes newly arisen from basal buds, the leaves are large, and the range of leaf size is therefore great. Superimposed on this is the plastic variation in leaf and shoot with differences in exposure.

Bright (1928) demonstrated that specimens from the top and foot of a slope on Hindhead Common, England, differed both in shoot length and leaf size, and in the proportions of tissues. This he attributed to differences in exposure. In a closely related species, *V. intermedium*, Ritchie (1955b) demonstrated within individual clones morphological differences which he ascribed to environmental differences.

Other workers, notably Avdoshenko (1949) and Zlobin (1961), have drawn attention to the structure of bilberry clones and in particular to the intertwining of different generations of bushes. Zlobin, by classifying the bushes into classes of form related to age (compare *Calluna*), showed that the proportions of the classes changed with time, the older gradually spreading from the centre to the periphery of the clone, bringing about its destruction.

There is some delay in the inception of rhizome in the seedling. According to Sylvén (1906), the (primary) rhizome does not appear until the third year at the earliest. Thereafter, it ramifies in the humus about the plant, growing more or less rapidly into the surrounding area. Everett (1967) gives figures both for the growth rate of the longest rhizome from seedlings into sawdust (30 inches—ca 76 cm—in nine years), and for the diameter of the plant (17 inches—ca 44 cm—in nine years). Rhizome from established stands of bilberry, however, may grow 40 cm a year, and Keso (1908) reports lengths of more than 40 cm from Finland. The net expansion of the stand is considerably less than this.

The morphology of the young rhizome has been adequately described, e.g. by Warming (1890), Grevillius & Kirchner (1923). The older rhizome is often contorted and is abundantly branched in its middle parts, whereas the young rhizomes may occasionally be strikingly straight. In soils with a mor layer, the old rhizome usually lies at the boundary with the mineral soil, younger rhizome being more superficial; cf. also Heath & Luckwill (1938). Old roots (equal in age with the rhizome) occupy the proximal end of the rhizome and may be exceedingly tortuous, descending deep (more than 45 cm) into the mineral soil. Roots on younger rhizomes are usually very fine and are concentrated to the upper part of the humus. The thickness of the rhizome varies greatly along its length, depending partly on age and partly on proximity to an aerial shoot or large root: as Kujala (1926) remarks, "...Oft ist von den grösseren Wurzeln aus aufwärts eine plötzliche Dickenzunahme zu beobachten." About bilberry stands a zone of advancing young rhizome may be seen, often in the upper part of the humus or in the litter, but occasionally in the mineral soil. Such rhizomes are remarkably uniform in age and diameter, usually lack aerial shoots, and may be orientated almost parallel (cf. *Pteridium aquilinum*: Watt 1947 a).

The branching of the rhizome, like that of the aerial shoots, is sympodial (Warming 1890, Kujala 1926), and the disposition of the aerial shoots reflects that of the rhizome. From their point of origin two rhizomes extend 20-30 cm underground without branching, then divide, ideally into two, occasionally into three or more, of which the middle one is the most vigorous. This middle rhizome turns upwards and develops a green shoot or continues its growth underground. After a further 20-30 cm it divides into a group of shoots which correspond morphologically with the green aerial shoot. Thus the rhizome in bilberry ends in a green shoot or in a corresponding group of rhizomes. Further growth is continued by two side branches (Kujala 1926). Hence it will be seen that the aerial shoots tend to arise at intervals of 20-30 cm along the rhizome; but cf. also Anderson (1961) for the scale of morphological pattern.

Anderson, who studied the structure of some upland plant communities in Wales, stated that on the sites studied by him, although the total length of any one rhizome might exceed one metre, the tiller-producing length (i.e. the distal part of the rhizome with living tillers) never exceeded one metre and rarely exceeded 90 cm (cf. Anderson 1961, Fig. 3). He regarded this as part of the "normal" pattern of bilberry. Keso (1908) reported from Finland rhizomes which had attained a length of 183 and 169 cm at the age of 21 and 15 years, respectively. The maximum age found was 32 years for considerably shorter rhizomes. Kujala (1926) reports Keso as having found rhizomes 200 cm in length, but considers this to be the maximum length attained. However, Avdoshenko (1949, p.197), citing Doroshenko (1925), gives a length of 800 cm, but no age; and the present author has excavated single rhizomes of up to 550 cm in length on several occasions (see Fig. 5, from Skogshögskolan; others from a mossy pine stand near Ballater, Scotland and from a similar spruce stand at Garpenberg, Sweden). In two cases, the rhizomes were almost devoid of aerial shoots (compare *V. vitis-idaea*).

Anderson also reported natural die-back in stands some 12 years old, and that few of the rhizomes more than 15 years old bore shoots with green leaves (cf. Zlobin 1961). Kujala (1926) notes that "Somit spätestens nach diesem Alter (15-32 Jahresringe) beginnt das allmähliche Absterben und Verwesen der Stengel und Rhizome, während die jüngeren Rhizomäste ihr Wachstum fortsetzen."

A rhizome unit is thus commonly two metres or more in length, has many branches, bearing on their distal part aerial shoots of various age, and is decayed at its proximal end. Although opinion is divided as to the average or the maximum length attained, there seems to be general agreement in the literature that the maximum age at the decayed end is in the region of 30 years, while the aerial shoot attains an age of 20-30 years. The true rhizome age may be greater, since annual rings may not be formed after an age of 30 years or so, although the rhizome may remain undecayed for some years thereafter.

The form of the stand

A characteristic form of the bilberry stand is that of an irregular, approximately circular patch between three and ten metres in diameter (cf. Serebryakov 1954). Smaller patches are also found, over a range of sizes. Many patches are centred on old, decaying stumps or on boulders. Even when an apparently uniform "carpet" of bilberry covers the ground, the constituent patches can often be distinguished in spring and autumn, either by differences in the time of leafing or by means of the strongly contrasting autumn coloration.

On some sites there is a perceptible increase in the density of stocking of the aerial shoots from the margin of the patch or stand towards the centre. This coincides with an increase in the rhizome density in the humus. Beyond the outermost aerial shoots there is a zone of pioneer rhizome, almost devoid of aerial shoots. This situation is thus largely analogous to that in *Pteridium aquilinum* (Watt 1947). The stand expands by rhizome growth at a rate estimated by Ritchie (1955a) to be five to ten centimetres a year (cf. Everett 1967). Here a distinction must be made between the rate of advance of the "patch" and that of the rhizome, the latter being considerably the greater. Both Ritchie (1955a), for *V. intermedium* and Oinonen (1967) for *Pteridium* in Finland have assumed for certain purposes that the rate of advance is constant, i.e. that there is a linear relationship between clone diameter and age. Thus clones of *V. intermedium* have been estimated to be 150 years old or more; similarly large stands of bilberry might, on the same assumption, be of comparable age, allowing for possible differences in growth rate. On theoretical grounds, as Kujala (1926) and others have pointed out, "...ist die Heidelbeere auf Grund ihres Wurzelsystems eine 'unsterbliche' Pflanze."

There is evidence from numerous sources, e.g. Perttula (1941), Kujala (1926), Södergård (1935), Ritchie (1956) that seedlings are uncommon in nature and that seedling survival is low. They occur nonetheless, and seem then to be associated with birds' excrement, cf. Kujala (1926); the fruits are an important part of the diet of many birds (Hegi 1927, Grevillius & Kirchner 1923) and animals (Heintze 1915, 1916). Although reproduction by seed may be instrumental in the initial establishment of bilberry on some sites, the overall impression is that vegetative reproduction predominates.

In sum, therefore, bilberry is a long-lived dwarf shrub, highly variable morphologically and apparently of complex stand structure, by numerous workers considered, like its North American relatives, to be clonal. Its longevity gives it a rather constant place in the vegetation of the forest floor, and it may persist, thanks to its rhizomatous habit, about stumps and boulders when the forest has been disturbed by fire or felling. It is not confined solely to forested sites, but is

Figure 1.
Schematic depiction of
structure in the bilberry
bush, after Zlobin (1961).
Original axes (black) are
dead; years of origin are
denoted 1, 2, 3... on the
primary, 1', 2', 3'... on
later axes. Living current
shoots shown by triangles.

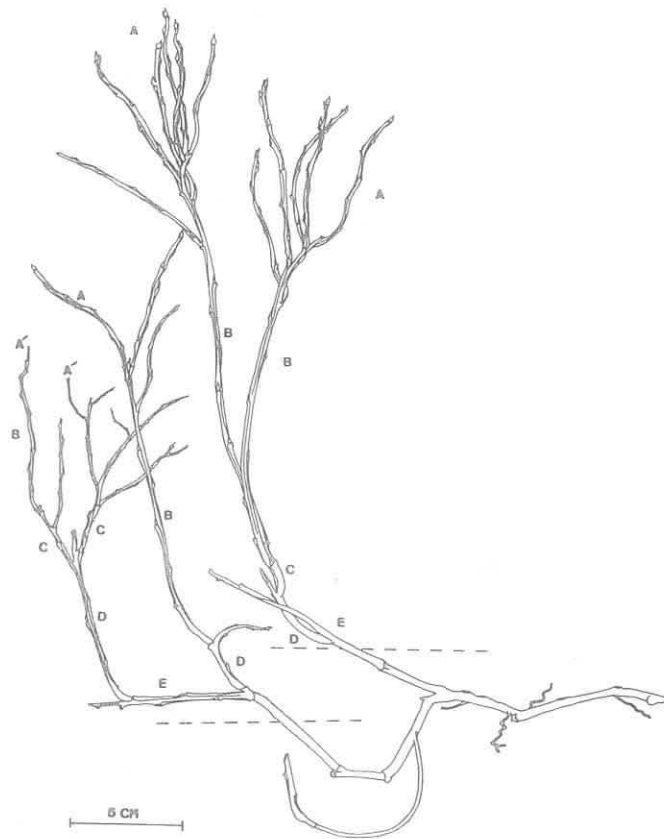
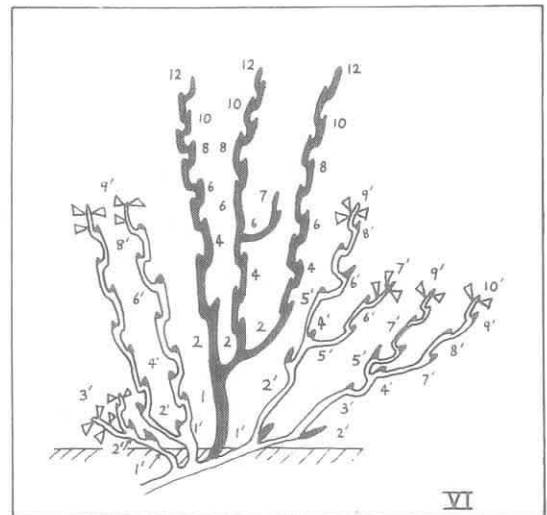


Figure 2. Tillers in bilberry. Right, two 6 year old vegetative axes (note long shoots B) arising from base E, the point of origin of the "individual". Left, an axis with short current shoots A' and between them, a younger vegetative axis. The long shoots B are the frame branches of the bush. Note incipient tiller on side branch of rhizome. Winter condition, December 1967.

also an important constituent of heath communities, both lowland and montane. On many forest site types it is dominant or codominant and may typify the site.

Yet relatively little is known of its population structure (but cf. Zlobin 1961) or internal dynamics, both of which are important if the part which it plays in the forest ecosystem is to be understood. There is intrinsic scientific interest also in elucidating its age structure and dynamics, since we know surprisingly little about these features even in annual plants, populations of which are fairly well defined. Processes of change in plants may be expressed qualitatively or quantitatively against a time scale, whenever the rate of change is such that they are perceptible. Changes in the number or distribution of individuals may be perceptible, even when the population is apparently stable — for there is evidence that stability, rather than instability, characterises vegetation to a remarkable extent (see e.g. Tamm 1948) even when change is great at the individual level. In rhizomatous plants there is difficulty in defining the individual; here the rhizome unit might be regarded as the individual, although it is scarcely amenable to treatment as such, since it can only with difficulty be excavated entire. For the purposes of population study, the individual is considered to be the aerial shoot or tiller.

Study of tillers may not be strictly analogous to the study of "true" individuals, in that the population structure of tillers may be determined by factors other than those which regulate numbers and distributions of individuals, i.e. rhizome morphology may primarily determine population structure. There may be similarities, but it remains to be seen in what way populations of quasi individuals resemble those of true individuals, as regards structure and dynamics.

Yield studies in uneven-aged stands of dwarf shrubs are notoriously difficult; therefore it is of interest to express population changes not merely in terms of numbers of individuals, but as rate of change in the production of plant material in both gross and net terms. In this way growth may be expressed in terms of the individual and the population. Subsequent comparisons of populations might then be made on a common basis, thus mitigating some of the sources of error inherent in such comparisons.

Only a few of the points raised here can be directly studied in the present investigation. To attempt immediately to study the bilberry community as a whole and to make comparisons between communities is probably futile, without a knowledge of the sources of error involved. The aim of this investigation is therefore to study isolated stands of bilberry in detail, to determine their structure and sources of variation, on the assumption that they are the basic unit of the community; and to discover a character

or characters in terms of which comparisons can be made. The following main questions will be asked :

- 1) What relation does the aboveground part of the stand bear to the underground ?
- 2) How do standing crop, production and performance vary throughout the stand ?
- 3) Can age be used as a common factor for comparing one population with another ?
- 4) Can differences presumed to exist in the growth of stands of bilberry on different sites be better expressed by the use of growth rate than by direct comparison of standing crop and production without regard to age ?

Methods

Field sampling

Selection of sampling unit

The field sampling method was designed for the following purposes: First, for studying the structure of bilberry stands, secondly, for estimating standing crop, and thirdly, for convenience in use. It was required to be capable of detecting small-scale variations in standing crop and of permitting these to be related both to one another and to the associated rhizome.

The morphology of the rhizome had therefore to be taken into account when the size of sampling unit was selected. While relatively large units, such as quadrats 50 x 50 or 100 x 100 cm, may be preferable to smaller units for certain purposes and under certain conditions, e.g. they may give better estimates less subject to bias, their very size may obscure vital differences in space. The analogy of the fishnet may be appropriate here. Since an analysis of the structure of the stand was the primary object of the study, the large quadrats were not used. Preliminary studies of the literature and of the rhizome (Anderson 1961; Kujala 1926—see Introduction) suggested that an appropriate quadrat size would be 25 x 25 cm, this being approximately equivalent to the distance between successive aerial shoots on a rhizome. A quadrat 10 x 10 cm was also used at first, but subsequently discarded, since it tended to be biased towards small tillers (cf. Anderson 1961). The 25 x 25 cm quadrat was convenient to handle in the field, which also contributed to its selection.

Sites investigated

The main investigation was confined to two fairly well defined forest site types, the one corresponding most closely to the "Frisk ristyp" (mesic dwarf-shrub type) of the Eneroth-Arnborg system (Arnborg 1953), the other to a transition between the "Torr-ristyp" (dry dwarf-shrub type) and the "Skarp ristyp" (very dry dwarf-shrub type) of the same authorities. It should be noted here that the system referred to is intended for use in northern Sweden and is therefore not strictly applicable to central Sweden; however, no generally acceptable system, covering the whole country, yet exists. Material was also collected for convenience from a site adjacent to the Royal College of Forestry, not corresponding to any in the Arnborg-Eneroth system, and from a sparsely wooded lowland heath in eastern Scotland (Cammachmore); these sites are described below.

Garpenberg (60° 18' N / 16° 11' E)

Garpenberg is situated at the southern edge of the topography characteristic of Norrland. The area with which the present study is concerned has been investigated from various aspects in the past, both by workers from the Royal College of Forestry (see, for instance, Troedsson (1956), Samuelsson (1960)), and elsewhere.

Five bilberry stands in all were studied, of which three only are discussed in detail here. All material was collected from the mesic site type described above, under stands of spruce. For a detailed description of the sites and the sampling lay-out, see the relevant Appendices.

Hamra (59° 12' N / 17° 58' E)

The name Hamra is a convenient designation for an area in Södertörn south of Stockholm, situated on the summit of a ridge of glacial material carrying a 50 - 60 year old self-sown pine stand, with a sparse understorey of spruce. Part of the area contains experiments in forest fertilisation, and has been described briefly by Holmen & Nömmik (1967).

Three bilberry stands were studied, of which two only are referred to here. The site as a whole is in marked contrast to the mesic site type at Garpenberg, having both a lower rainfall and being excessively drained. For details, see relevant Appendices.

Cammachmore (57° 3' N / 2° 11' W)

This site is on the Elsieck House Estate, ca 3 km from the sea on the Kincardineshire coastal plateau in eastern Scotland. The bilberry stand studied is growing under a stand mainly of birch, aged about 100 years. The area might be characterised as relict wet heathland, forming an enclave in land otherwise used for agricultural purposes. For details, see Appendix.

Skogshögskolan (59° 25' N / 18° E)

This site is on the west-facing slope of a steep, rocky ridge overlooking Brunnsviken, an almost land-locked inlet of the Baltic in the northern part of Stockholm. The forest stand is a mixture of hardwood and conifer, mainly oak and Scots pine with an undergrowth of rowan, cherry, birch and other species. Bilberry stands occur frequently, being generally pure and clearly defined in the oak-dominated part of the forest from which material was collected. For details, see Appendix.

Sampling layout

Sites studied in detail were mapped. The bilberry stand, and adjacent plant communities were mapped in detail, and the map was then used as the basis for the sampling layout.

From a point taken at random on an arbitrary baseline, a belt transect consisting of contiguous 25 x 25 cm quadrats was laid out, normally one transect in each stand, in such a way that no tree was in the path of the transect. In some cases quadrats were laid out at regular intervals on half of the transect, e.g. G/IV, followed by contiguous quadrats in the other half. This was intended to test whether an adequate picture of the structure of the stand could be obtained by means of a smaller number of samples than that involved in sampling by contiguous quadrats.

In addition to the main transect, both random quadrats (allocated by a grid system) and quadrats at fixed intervals along lines at right-angles to the margin of the stand were used. The origin of the short lines was determined arbitrarily.

In addition to the complete belt transect, its shorter counterpart the "ladder" (Pearsall & Gorham 1956) was used. The advantage of the transect of contiguous quadrats is that the error due to edge effect (particularly marked with small sampling units, and especially so in stands of this type) is mitigated. A further advantage is that spatial pattern can be detected and depicted with fair accuracy in diagrams. Excavation of rhizome is facilitated, and since the origin of the transect is outside the stand, it is easier to place the first quadrat objectively. This is true also of successive quadrats, the origin of which is determined by the clearly defined edge of their predecessor. There is considerable difficulty in avoiding bias when laying out small quadrats in dense stands of dwarf shrubs. (For layout, etc., see Appdx III).

Collection of material

All stems of bilberry, cowberry (*V. vitis-idaea*) and ling (*Calluna vulgaris*) within a heavy angle-iron quadrat frame were severed with secateurs at the top of the moss layer and placed in a labelled bag. Only stems arising within the area of the quadrat were clipped. The edge of the block (consisting of the moss or litter layer, any low herbs not clipped off with the shrubs, the humus and the mineral soil to a depth of ca 40 cm) was then severed as cleanly as possible with a sharp machete and the whole was lifted out. The "north" edge of the block, farthest from its origin in the "south-west" corner, was marked with plastic tape to facilitate orientation in the laboratory. Rhizome and roots remaining in the hole were removed and placed, together with the bag of aerial shoots, in a plastic sack with the excavated block. An effort was made to ensure that the sides of the hole were as nearly vertical as possible. The thickness of the humus layer was measured on the north edge of the hole.

As soon as possible after arrival at the laboratory, the material was dried at 105°C and weighed. It was then separated into fractions intended for the following five purposes :

- 1) Study of rhizome morphology and age,
- 2) Study of standing crop and stand structure,
- 3) Study of the age and development of individual aerial shoots,
- 4) Study of performance and variation in leaf weight and size, shoot length, etc.,
- 5) Study of the mineral nutrient content of the aerial shoots.

Complementary information for each site (viz. vegetation, soil, history, etc.) is given in Appendix II, in which reference is also made to other sources of information.

Complete species lists for each quadrat, data on humus thickness, standing crop of aerial shoots and rhizome by fractions, numbers and distribution by length of current and older shoots, ages, etc., are available in stencil form from the Section for Plant Ecology, if required.

1 Age structure

1.1 Age structure of the rhizome

1.10 Introduction

The form and extent of the bilberry stand are determined by the growth of the rhizome; hence the configuration of the aerial part of the stand should be explicable in terms of the underground part. It is therefore necessary to study first the age structure of the rhizome, so that the relationship of the aerial to the underground part can be more easily understood. Since the outer part of the stand is the most accessible, it is intended to show how it is built up, then to apply this knowledge for elucidating the structure of the inner part.

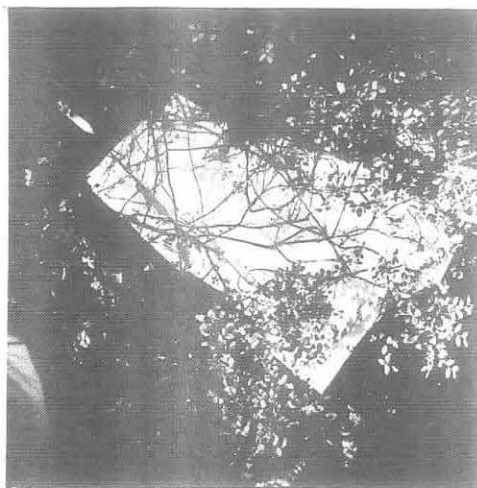
1.11 Rhizome growth direction

Two methods were employed in preliminary studies of rhizome growth. In the one, a belt transect was excavated and removed entire to the laboratory for dissection. The position of as many aerial shoots as possible was plotted and their age was determined either by count-backs or by sectioning (see Appdx I). Then the transect was dissected from above and the rhizomes were mapped and aged, the growth direction of the tips being noted. A plan of part of stand G/I, on which this method was used, is shown in Appendix III. The disadvantage of the method is that in order to obtain complete rhizomes, the transect must be at least a metre wide, which renders it unmanageable. On less wide transects, so many rhizomes are severed that the results are difficult to interpret. The other method, used more frequently, is to excavate a single rhizome system *in situ* and to map the position of tillers and rhizome branches. Figure 5 shows an excavated rhizome system from Skogshögskolan, while Fig. 3 and 4 are vertical photographs of the exposed rhizomes; the main rhizome is marked by arrows. These photographs give an impression of the general alignment of rhizomes and their complex intertwining. The general direction of growth was centrifugal, although branches from adjacent rhizomes crossed at a large angle.

Table 1 shows total lengths and percentages of rhizomes which made an angle of 45° or less with the mid-line of belt transect H/III-1, and which were growing away from the centre of the stand.

Quadrat No.	Total length cm	Length small rhizome cm	Small $\leq 45^\circ$	%
1-5 Distal	1600	1400	1200	85
6-10 Prox.	7300	3600	3000	83

Table 1. Growth direction in rhizome less than 1.5 mm diam., H/III-1. Length to nearest 100 cm.



Photos C. O. Tamm

Figure 4. Vertical photograph of rhizomes in situ in the interior of stand S/III, corresponding to square C 2 of Fig. 5. Arrows show main rhizome. Compare Fig. 3 (right).

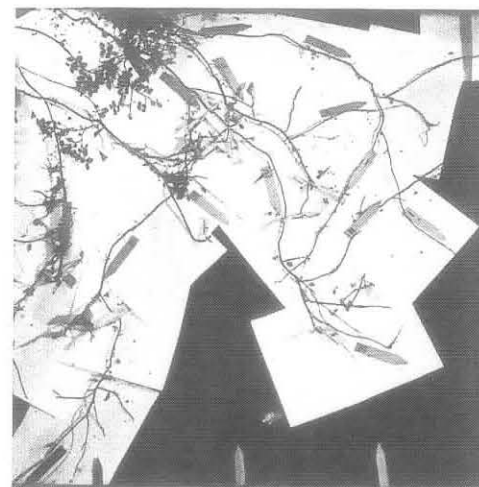
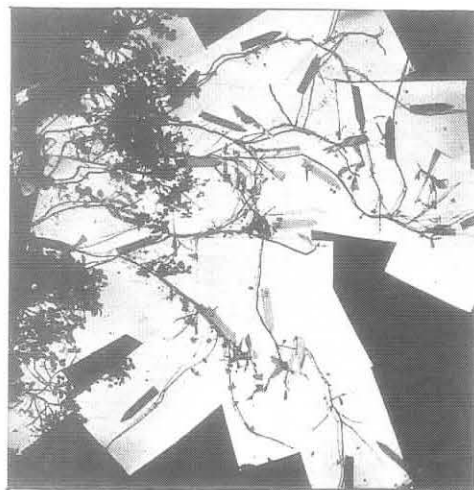


Figure 3 a, b. Vertical photographs of rhizome in situ in marginal zone of stand S/III, corresponding to squares F, G, H 4 & 5 of Fig. 5. Numbered plastic labels mark tillers, removed to facilitate photography of the rhizome. Compare Fig. 4 (left).

The growth direction of rhizome of large and intermediate diameter was not assessed in the same way, but seemed to be mainly centrifugal. Little large rhizome was present, but intermediate rhizome made up about half the total length of rhizome on quadrats 6-10 (interior). Since the growth direction of the rhizomes was assessed quadrat by quadrat, some errors in length measurement and in judging the angle may be involved. The figures for rhizomes growing centrifugally may be too high, but it is concluded that the primary growth direction is centrifugal.

This is in agreement both with casual observations of the manner of spread of bilberry stands and with the results of e.g. Zlobin (1961), Ritchie (1955a) and Everett (1967). It is of interest here that the proximal end of the rhizome shown in Fig. 5 was still attached to other rhizomes which were both demonstrably growing in the opposite direction (from the decaying tree stump in the centre of the stand), and which had living aerial shoots in their distal parts.

Another interesting point is that the "straight-line" length of the main rhizome in this case was ca 350 cm, whereas the true length was ca 520 cm. It is evident that a calculation of growth rate, based on age and true length, would give a very different result from that based on the distance along a transect from the rhizome tip to the age maximum, e.g. from H4 to A4. The latter, however, represents the net rate of advance of the rhizome, which is probably the more relevant in practice.

1.12 Relationship between diameter and age

Figure 6 shows the relationship between rhizome diameter and age in material from Garpenberg. The material is based on rhizome of diameter greater than 1.5 mm, on the assumption that diameter increases with age: the purpose of sampling was to discover the oldest rhizome on each quadrat. Hence the lower boundary is artificial, while the irregularity of the upper reflects the effect of a large root or tiller on rhizome diameter (cf. Kujala 1926). The maximum age of rhizome in this material was 28 years.

Diameter growth remained fairly constant over the period for which material was available, showing no tendency to decline with age (contrast Fig. 7 and aerial shoots). This impres-

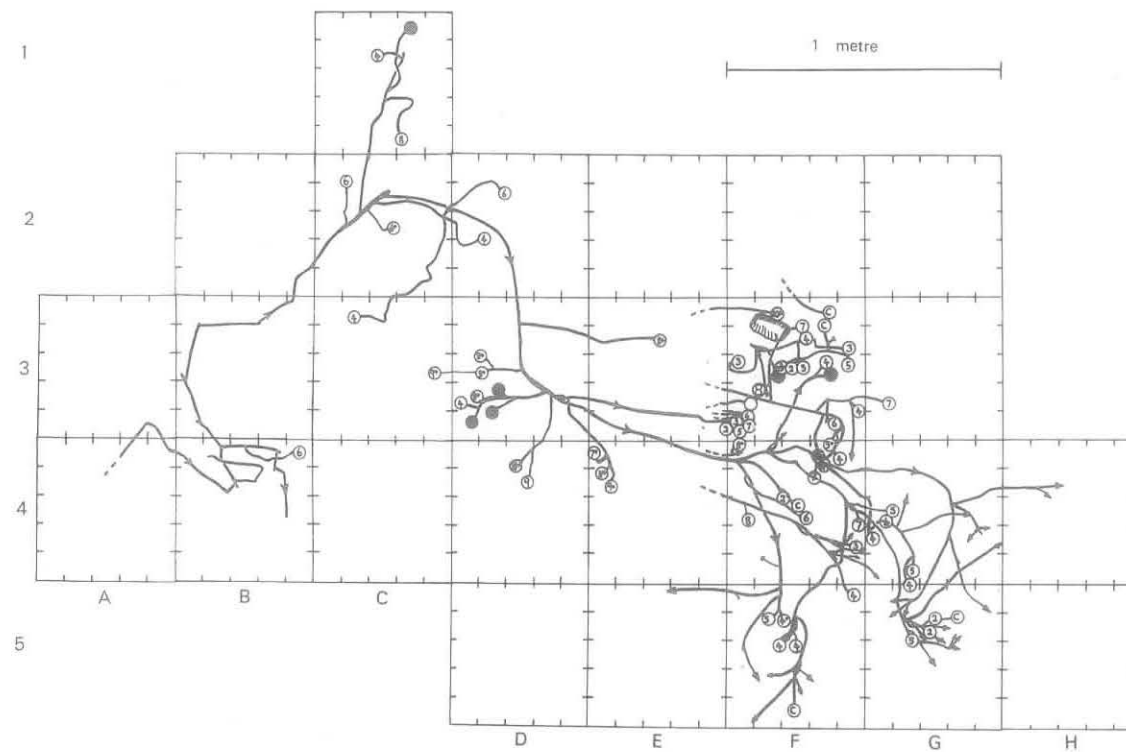


Figure 5. Excavated rhizome system *in situ*, showing position and age of tillers, S/III. Open circles with figures are living tillers + age, filled circles are dead tillers of unknown age. The oldest tillers (D 3) were ca 15 years old according to ring counts. Note branching of rhizome (C 2). Origin of stand in decayed stump in A 4. The object in F 3 is a boulder. Cf, Fig. 3-4.

sion is further supported by ring analyses, which indicate that over the range of age studied, although radial growth varied from year to year, there was no decreasing trend comparable with that shown by the aerial shoots.

Figure 7 shows rhizome diameter growth at Hamra (mainly H/II). Growth was initially similar to that at Garpenberg, but was consistently less after the sixth year. Few rhizomes older than 15 years of age were present, and the maximum age found was 23 years. This difference may not be real, in consequence of errors in determining age by counting rings. Nevertheless, the maximum diameter of the rhizome in the Hamra material was less than 4 mm, compared with more than 6 mm in the material from Garpenberg. There seemed to be a tendency for the rate of diameter growth to decrease with age, again in contrast to the Garpenberg material. There were marked differences in the thickness of the humus and litter layers between the two sites, although the total length of rhizome on a quadrat differed comparatively little. Hence the volume of humus (including litter) available to a given length of rhizome must have been considerably less at Hamra than at Garpenberg.

1.13 Progression of rhizome diameter

Figures 6 and 7 show clearly that rhizome diameter increases with age. Since growth appears to be primarily centrifugal, the absolute weight, and the proportion of rhizome of large diameter should increase from the periphery towards the centre of the stand.

Figures 8 and 9, which show for the material from Garpenberg the progression by weight of the three diameter classes of rhizome, demonstrate first, that the weight of the rhizome of large diameter increases from the periphery towards the centre, and secondly, that its maximum weight is not attained at the centre. Total rhizome weight did not reach a maximum at the centre.

As was noted above, the maximum age of the rhizome was 28 years. Rhizome older than this age was dead and decayed. The maximum age was measured invariably either immediately before a decayed end, or before an end exhibiting traces of insect larval galleries. Therefore, the weight of rhizome of large diameter might be expected to decrease after the point representing the maximum age.

1.14 Progression of rhizome length

Figures 10 and 11 show the progression by quadrats of rhizome length in each diameter class. In general, the sequence of increase is the same as that exhibited by weight, but the relationship of the large to the small-diameter rhizome is brought out more distinctly.

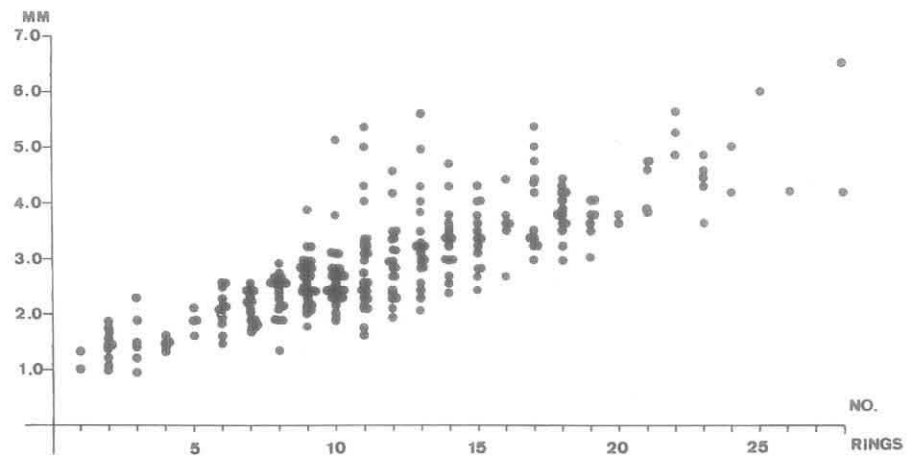


Figure 6. Diameter growth of rhizome (under bark) at Garpenberg. Based mainly on rhizome in medium and large diameter classes.

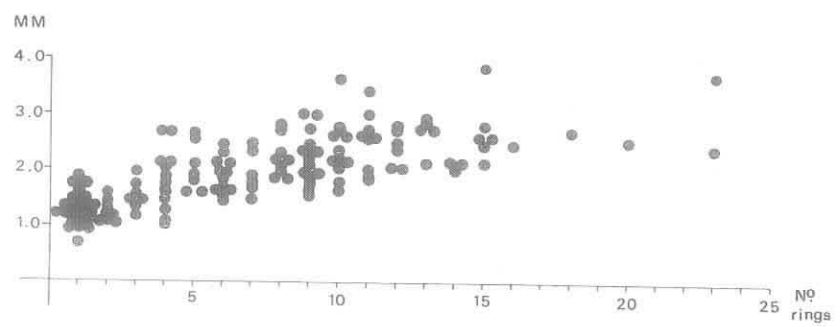


Figure 7. Diameter growth of rhizome (under bark) at Hamra. Based mainly on medium and small diameter classes, there being little large-diameter rhizome.

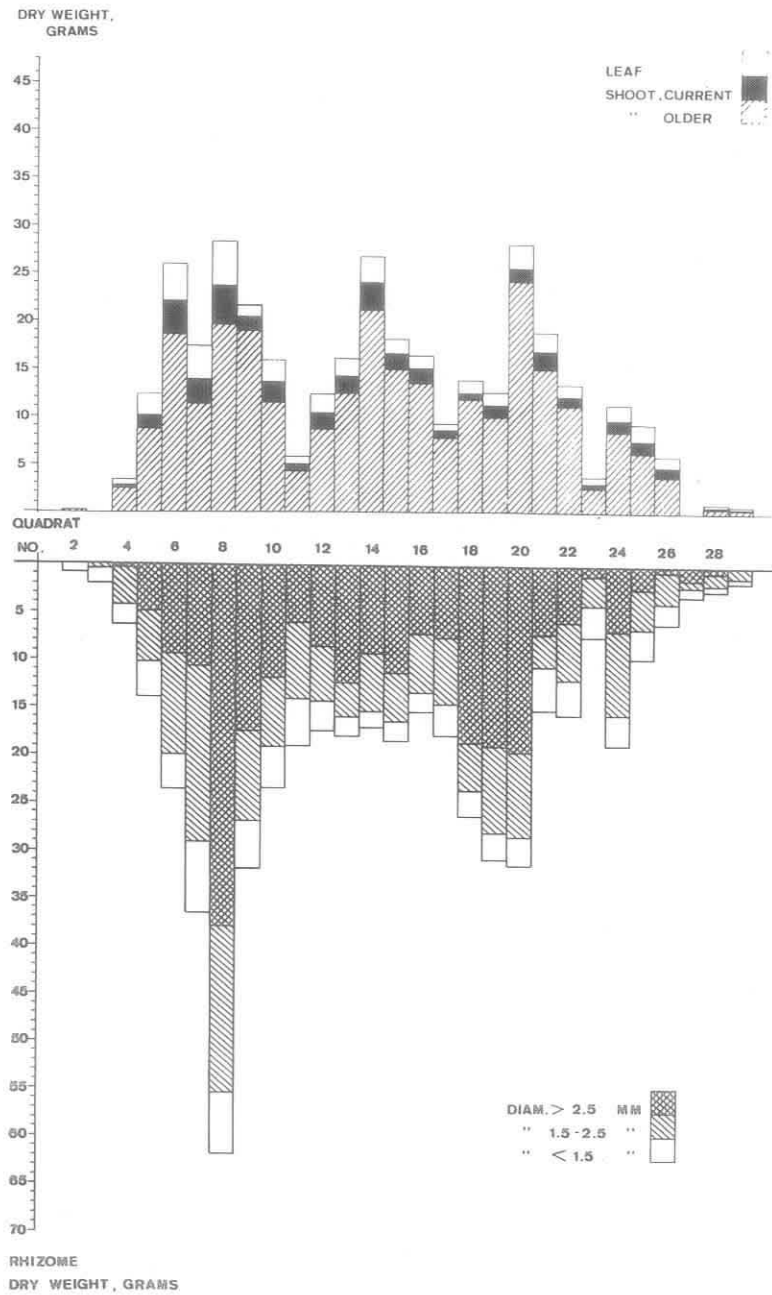


Figure 8. Progression of aerial and underground standing crop along the transect through G/III, 1966.

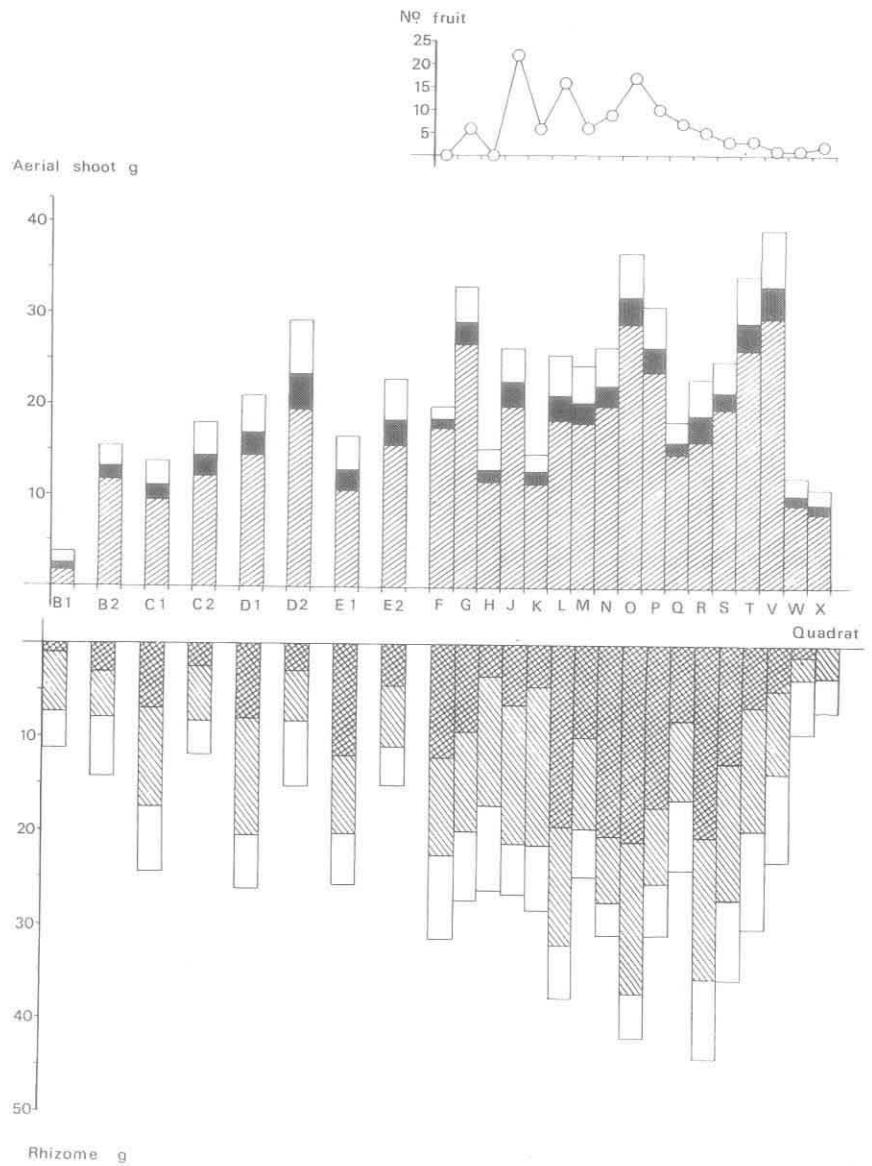


Figure 9. Progression of aerial and underground standing crop along the transect through G/IV. Quadrats B-E 1966, F-X 1967. The leaf weight for 1966 was probably underestimated, as a sharp frost occurred during sampling. Note numbers of fruits for 1967, and the gradient across the stand from B to X.

Figure 12, which shows for H/II the progression of rhizome length, is less clear but seems to follow a similar pattern. The division of rhizome into the diameter classes used may be less biologically appropriate at Hamra than at Garpenberg.

The peaks for the small rhizome represent an abundance of small rhizome; they are both more pronounced and more complex than morphological considerations suggest. Small rhizome is mainly associated with the distal part of the rhizome unit, since few old rhizomes have young branches arising directly from them. There appears to be more young rhizome in these zones than can be accounted for by the young "primary" branches of the rhizome. It is therefore probable that there is a second generation of rhizome present, overlapping the outermost. This is in general agreement with observations on excavated rhizomes, and is brought out by Fig. 13. In this stand (H/III), because of the sparseness of the vegetation into which invasion was taking place, stages in the formation of the closed stand could be distinguished. The number and length of small-diameter rhizomes increased from quadrat 1 to 5, in which the length, and the number, doubled. Intermediate rhizome increased to a peak in quadrat 7; the "front" of small rhizome in quadrat 5 probably represents branches arising from this rhizome. The increase in small rhizome in quadrat 7 is another "front", arising from rhizome in the region of quadrats 9 and 10, while the peak of small rhizome in quadrats 9 and 10 may be analogous to that in quadrat 5. In other words, what might be called a "primary front" is followed by another, probably related to the branching of the rhizome units of which the primary front represents the distal end. (Cf. Anderson 1961).

1.15 Rhizome age structure

It is difficult to determine precisely the position of the maximum or minimum for any of the rhizome diameter classes, because of the artificial interruption of the continuous sequence by the sampling units. However, the succession appears to be similar in all cases studied here. It remains to demonstrate that the weight maxima for the large rhizome are associated with the age maxima.

Figures 14 and 15 show the age of the oldest rhizome and aerial shoot on each quadrat. The pattern of distribution of these ages is striking. In neither G/III nor G/IV is the maximum age attained at the centre. The increase in age from the margin to a point some distance into the stand is marked in both stands, and especially in G/IV the decrease in age at the centre is noteworthy. In H/II, the maximum age (23 years) was attained at the centre (quadrats 13 - 14), while quadrat 20 had an age of 20 years. These figures should be compared with Fig. 8, 9, 10 and 11, and Appdx III (Fig. 2).

Figure 16 shows that the weight of large rhizome (>2.5 mm diam.) is related to the maximum age of the rhizome on each quadrat (cf. Fig. 3, Appendix III). Comparison with the other diagrams indicates that the age maxima for the large rhizome are followed by a decrease in

the weight of large rhizome. It is therefore probable that the two are related by the rhizome, the decayed end of which is at this point. Old (large) rhizome is present after this point, which is not physically attached to the large rhizome of the outermost unit. This suggests that it is part of the second generation of rhizome, the existence of which was inferred from the pattern of the small rhizome. With this rhizome should be associated a tiller system; it now remains to study the relationship of the aboveground part of the stand to the underground.

1.2 Aerial shoots

1.20 Introduction

Evidence in the literature (see Introduction) suggests that the aerial part of the bilberry plant may not occupy more than the distal end of the rhizome, 90 - 100 cm at most. It is, however, conceivable that this should vary in relation to the length or age of the rhizome unit. The progression of tiller age will take place in this distance and may represent in time 15 - 20 years or more. The youngest tillers should occupy the outermost part of the rhizome, inside the zone of pioneer rhizome, while the oldest should be near the middle of the rhizome unit. Older bushes may be present only as decaying shoot bases. Evidence in the foregoing sections was interpreted as indicating that there is an overlap between the outermost and the next rhizome unit. Hence the youngest tillers of the latter will accompany the older tillers of the outermost unit, giving rise to a complex age structure.

1.21 Age progression of the five largest stems

Figures 17 a-c show the distribution of the ages of all tillers measured in H/II, G/III and IV. Older tillers increased in frequency from the margin of the stand towards the centre. The age range on a quadrat was small at the margin, but wide in the interior. In all three stands, the oldest tillers were near the centre, although in G/IV old tillers were also found nearer the margin. The distance of these tillers from the distal end of the outermost rhizome unit is not in accordance with the supposed length of tillering rhizome (Anderson 1961). If Anderson's conclusion has general validity, it might be concluded that all old tillers farther than about a metre from the margin of the stand do not belong to the outermost rhizome unit. If, as suggested above, the tillering part of the rhizome varies in length in relation to the total length of the rhizome (e.g. the case of the 800 cm rhizome reported by Doroshenko (1925)) or age, this conclusion would not be valid.

Although there is some evidence in support of the suggestion of a variable relationship between total length and tillering length (this being related to the age of the rhizome), in the present case it is considered that the distribution of tiller age maxima indicates that several rhizome units are involved. This view is supported by excavation, and further evidence is presented below.

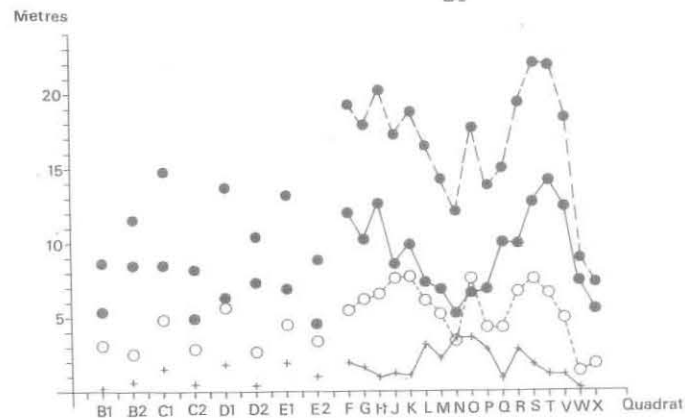


Figure 10.
Progression of
rhizome length,
G/IV. Quadrats
from 1966 on
left (B-E).

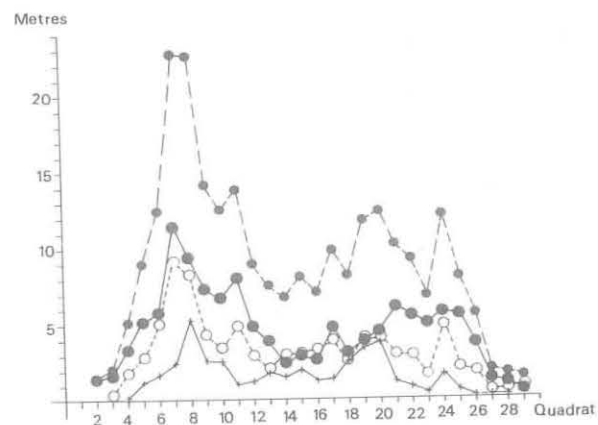


Figure 11.
Progression of
rhizome length,
G/III.

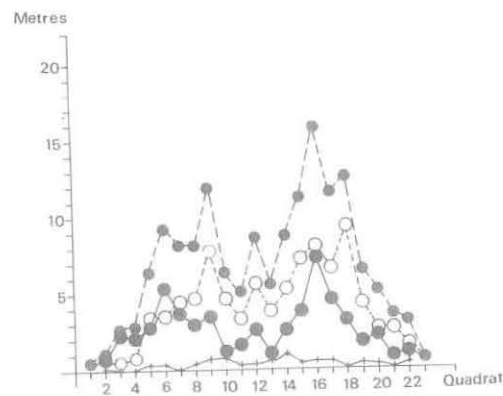


Figure 12.
Progression of rhizome length,
H/II.

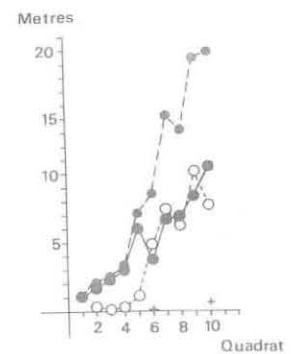


Figure 13. Progression
of rhizome length, H/III
(part).

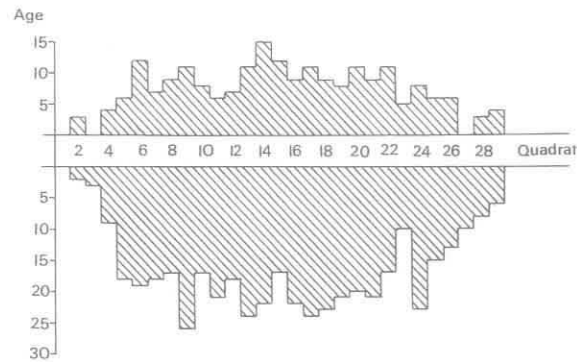


Figure 14.
Age of the oldest
stem and rhizome
on each quadrat in
G/III.

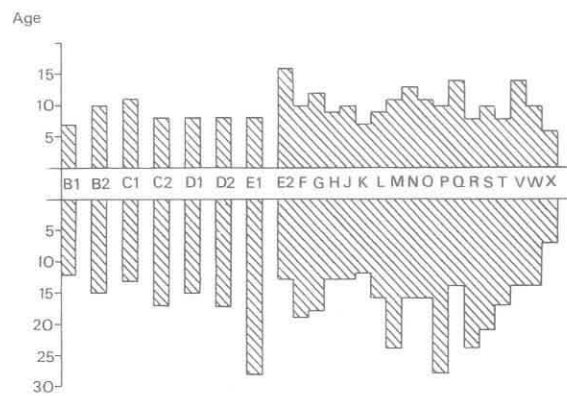


Figure 15.
Age of the oldest
stem and rhizome
on each quadrat in
G/IV.

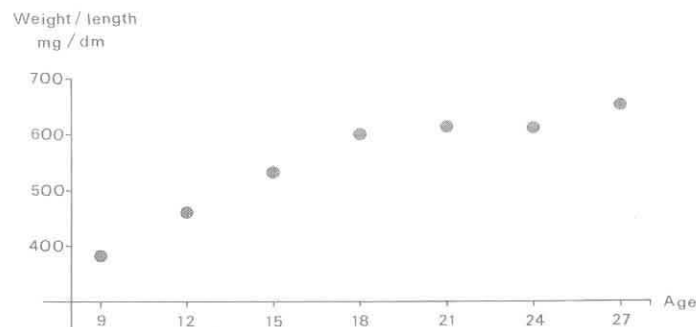


Figure 16. Relationship between weight of large rhizome and age of oldest rhizome, Garpenberg. Mean values by quadrats, mg / dm, by three-year age groups. Cf. Fig. 8-9 and Appdx III, Fig. 3. Note that "large" rhizome enters that class (>2.5 mm) only at an age of ca 8-9 years.

1.22 Relationship between diameter and age

The tiller base differs from most of the aerial shoots, in that it is terete. For this reason, basal diameter was measured on TS at the same time as the annual rings were counted. On each quadrat the five tillers with the largest basal diameter over bark were sectioned, and it is on these that the regressions of diameter on age in Fig. 18 are based. For details of measurement, see Appdx I.

At Hamra, the maximum age attained by the tillers studied was ten years, while at Garpenberg it was 15 years. The rate of diameter growth was greater in the Garpenberg material by about the fourth year and continued greater until the eighth year. There was insufficient material for valid averages to be calculated after the eighth year at Hamra and the twelfth year at Garpenberg. Nevertheless, the trend is clear; growth rate on both sites had begun to decrease by the eighth year. The material is considered to be representative of the tiller populations in the stands sampled, and therefore to reflect the general course of development. There was, however, great variation in the diameter attained by tillers of the same age; see, for instance, the scatter diagrams Fig. 38, 39 and 40. This problem is discussed in detail in section 3.

Figure 18 also shows the regression of basal diameter on age for the tiller populations of Cm I and II. The inclusion of this material in the same diagram as that from Hamra and Garpenberg might be considered unjustifiable, in view of the different status of the majority of tillers, i.e. their not being amongst the five largest stems. The age structure of these populations exhibits characteristics which agree closely with those of the five largest stems taken as representative of the populations of the stands as a whole. Evidence brought forward in a later section is considered to justify fully the direct comparison of these populations.

The course of diameter growth in the Cammachmore material is less well illustrated in the earlier years than that of the other material. It seems, however, that the initial basal diameter was of the same order in the entire material. Tillers in the Cammachmore populations seem to have grown rather more slowly in the first five years than those at Garpenberg and at about the same rate as those at Hamra. By the age of six years the average basal diameter had exceeded that at Hamra and was of the same order as that at Garpenberg. By the ninth year, when the rate of diameter growth of the Hamra and Garpenberg material had markedly declined, at Cammachmore it showed no sign of decrease and the average diameter was slightly greater than that at Garpenberg. Diameter growth rate showed no sign of decrease even in the seventeenth year, although it had clearly decreased by the thirty-fourth year. Since, however, there was no material between these two points, no conclusion can be drawn as to the point at which decline sets in. The 34 year old tiller was still vigorous and would probably have continued to grow for several years more, which seems to point to a

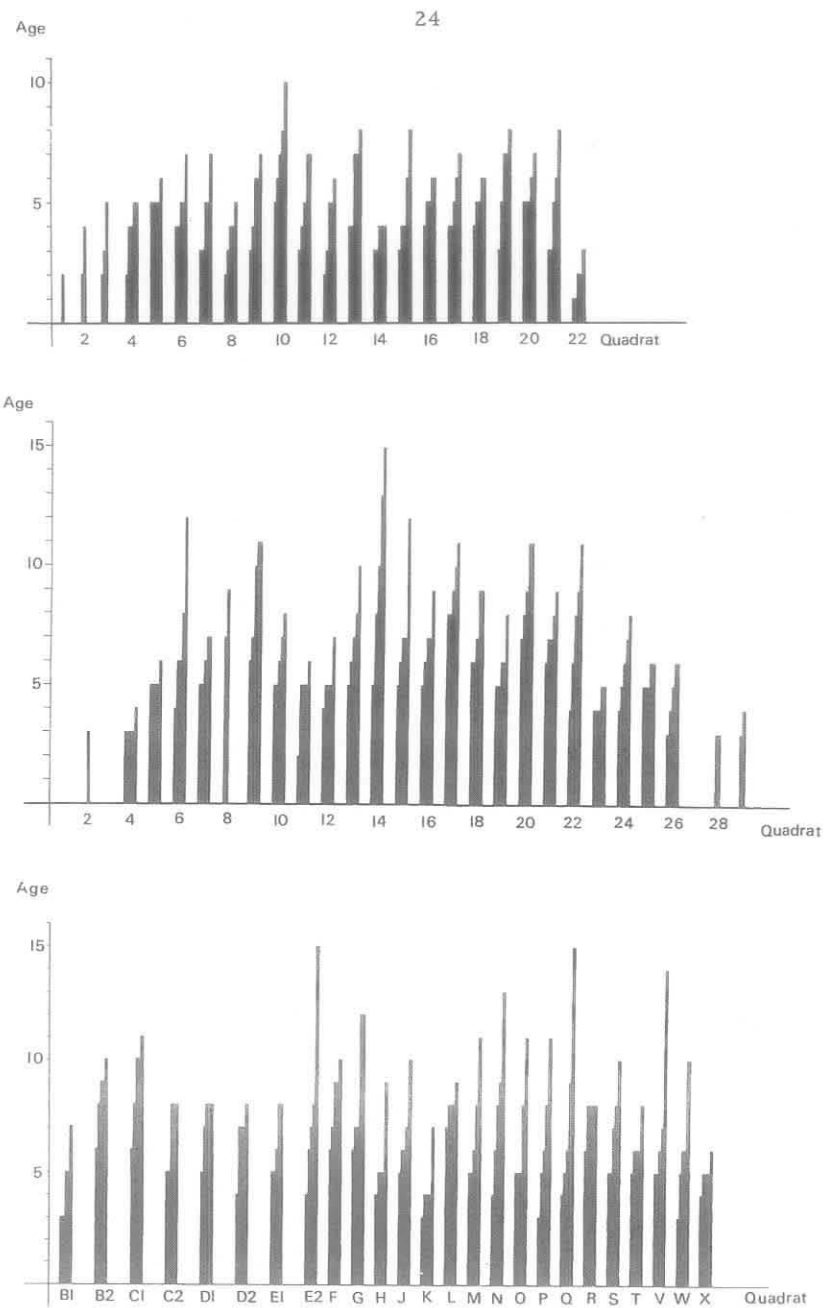


Figure 17. Distribution of the ages of the five largest stems on each quadrat in (top) H/II, (middle) G/III, (bottom) G/IV. Note the spacing of the quadrats B-E in G/IV.

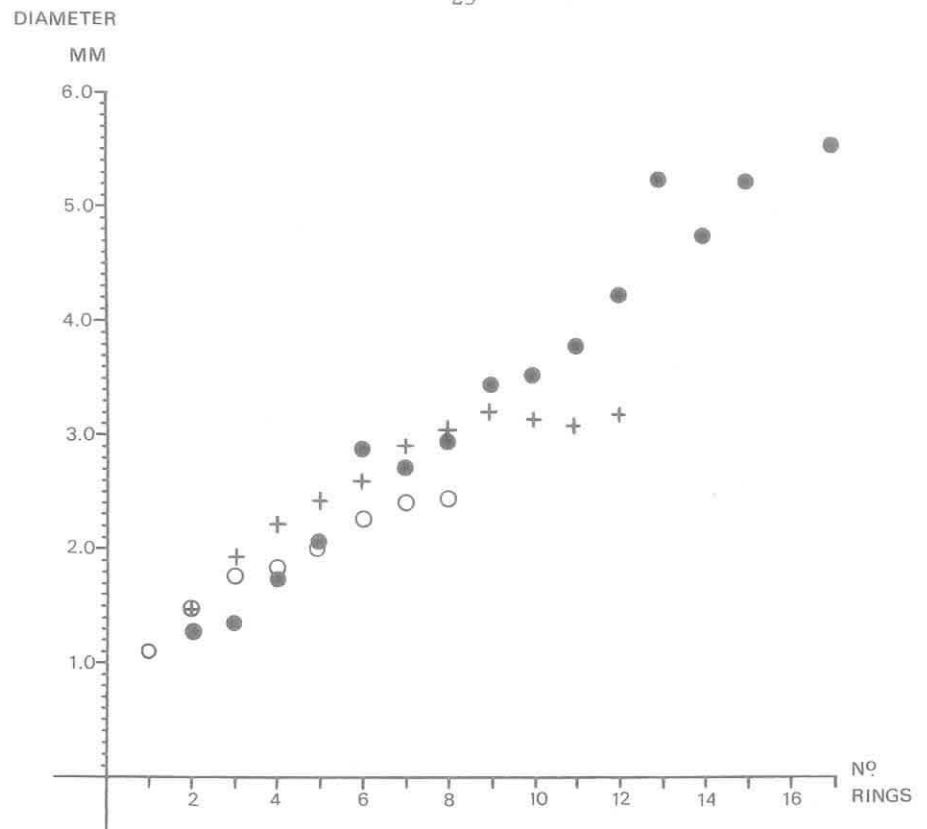


Figure 18. Diameter increment in aerial shoots at Hamra (open circles), Garpenberg (crosses) and Cammachmore (filled circles), mean values for the total population on the two quadrats at Cammachmore, for the population of dominant stems at Hamra and Garpenberg.

relatively sustained rate of diameter growth. The final average diameter of the tillers was considerably greater at Cammachmore than at the other two sites, and the difference in the final diameters between Cammachmore and Garpenberg was greater both absolutely and relatively than that between Garpenberg and Hamra.

1.23 Relationship between basal area and age

The age of the aerial shoots increases from the distal to the proximal part of the rhizome, and diameter increases with age. Hence the basal area should increase on each successive quadrat. Since the total basal area attained by the five largest stems on any site is probably a function of time, it should be related to the age of the oldest tiller on each quadrat. If the youngest tillers on the second rhizome unit follow the oldest on the outermost unit, without overlap, the basal area of the five largest shoots (BA_5) should decrease. If, however, the two overlap for a part of their length, BA_5 might be expected to remain constant or to decrease slightly. Total basal area (BA_{tot}), i. e. the sum of the basal area of all tillers on a quadrat, might be a better measure of this, but is less conveniently determined.

Figure 19 shows the regression of BA_5 on the age of the oldest tiller on each quadrat at Hamra and Garpenberg. Basal area and maximum age are correlated, although there is considerable scatter in the Garpenberg material (filled circles). The average BA_5 was greater at Garpenberg than at Hamra. The anomalous position of the oldest quadrats at Garpenberg is difficult to explain. Basal area is a more constant characteristic than weight, because even when the bush has been reduced to a skeleton, and hence has decreased greatly in weight, basal area remains unaffected. However, once decay has gone beyond a certain point, basal area, too, will be affected, in that the tiller will not be available for sectioning. It is therefore uncertain whether the anomaly is to be attributed to a loss of basal area consequent upon the total decay of tillers, or whether it results from the superimposition of young tillers of small diameter on older tillers, i. e. an overlap.

1.24 Progression of BA_5

The histograms in Fig. 20 show the progression of basal area into the stand. Basal area (BA_5) increases from the periphery into the stand. In some stands the increase is more gradual than in others, but the relative uniformity of BA_5 , once the closed stand has been reached, is noteworthy. Isolated peaks exist, but with few exceptions, these rise little above the general level. As is to be expected from Fig. 19, the Hamra stands have throughout a lower BA_5 than the Garpenberg stands. Except in the outer part of the stand, there

is little indication of any relationship between BA_5 and age, although this is clearly demonstrated elsewhere (Fig. 19, 22).

The relative uniformity of BA_5 in the closed stand is of interest, as also the relationship between this and BA_{tot} . This is further discussed in section 2.

1.25 Progression of standing crop

Figures 8 and 9 show the progression of standing crop aboveground and underground in G/III and IV (see also Appdx II). In both cases, the irregular profile is striking, even though there are indications of a gradual increase from the margin into the stand in G/III. Comparison of these histograms with those for age and BA_5 shows that there is no clear agreement between standing crop and these characters. However, Figure 21, a scatter diagram of standing crop (aboveground) on BA_5 by classes of age, brings out the underlying relationship. The scatter of the values tends to increase with increasing BA_5 , but on the whole, the relationship is reasonably clear. Figure 22 a-c shows for the same material (a) aerial standing crop on BA_5 , mean values by age groups (see Fig. 23), (b) aerial standing crop on age, mean values by age groups and (c) BA_5 on age, mean values by age groups.

Standing crop appears to increase linearly on BA_5 , as does also BA_5 on age. However, the regression of standing crop on age has a curvilinear tendency. This is not unexpected, since, for reasons outlined above, it is probable that the loss of weight with increasing age would be more marked than the loss of basal area from a population. It is somewhat surprising that the curvilinearity is not more pronounced, although this may be due to the fact that the maximum age in the material was only 14 - 15 years. The presence of younger tillers may also have contributed to the relatively slight decline.

In the case of the regression of BA_5 on age, it is conceivable that the relationship should be curvilinear. By analogy with forest stands, a maximum basal area might be attained when the site is fully occupied, independent of the density of stocking. Hence, when the tiller stand reaches full stocking, as it might be expected to do by a certain age, BA_{tot} should fluctuate about an equilibrium level. It is, however, necessary to study more closely the internal relationships within a quadrat population before further light can be shed on this question.

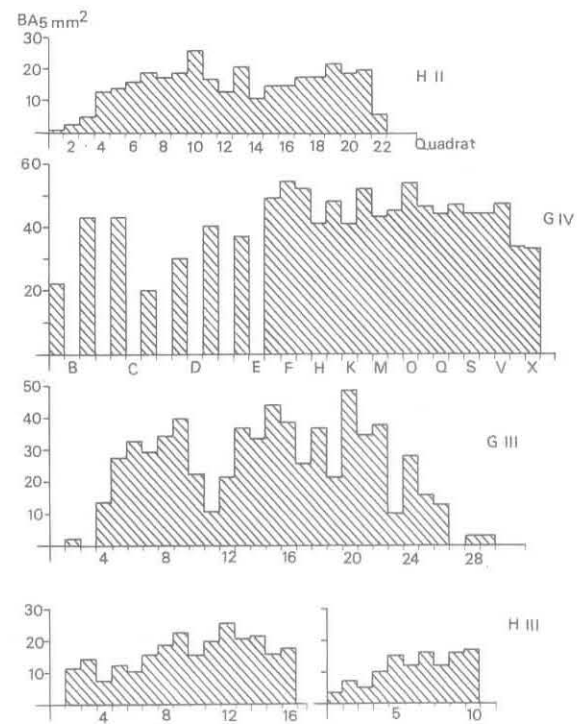
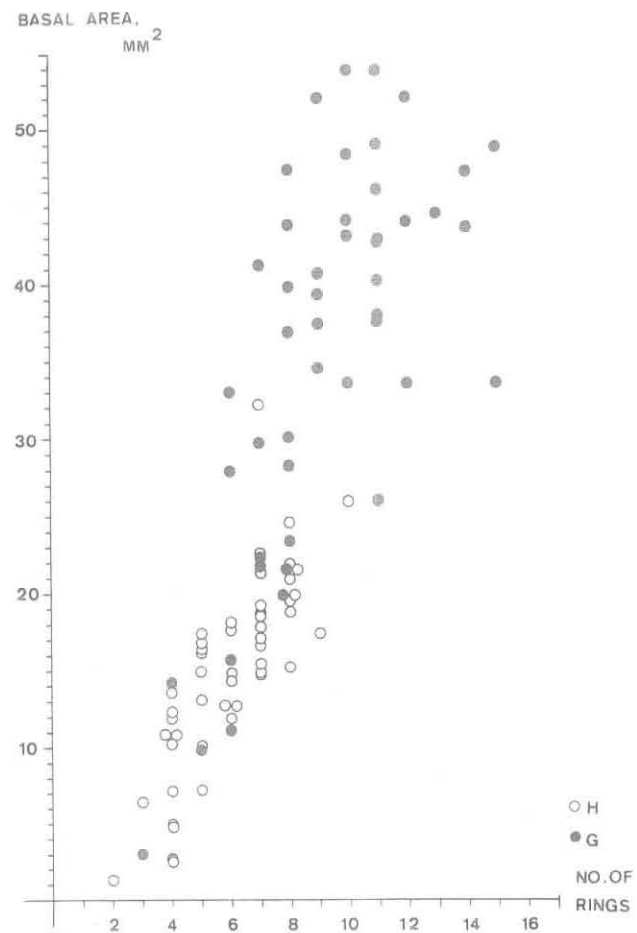


Figure 20 (above). Progression of the basal area of the five largest stems, Hamra and Garpenberg.

Figure 19 (left). Relationship between BA₅ and age, Hamra and Garpenberg.

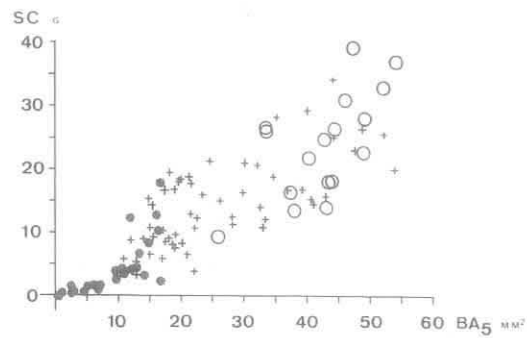
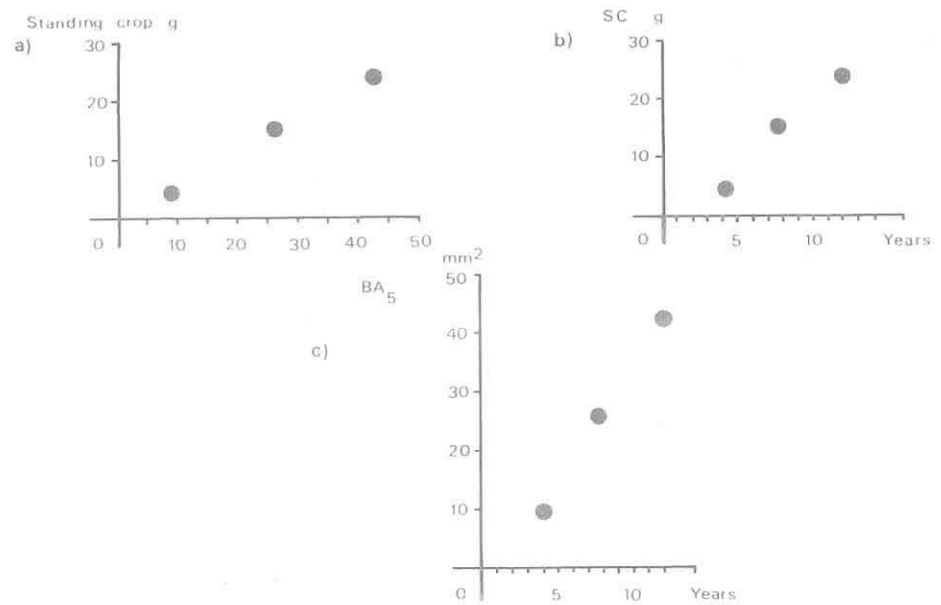


Figure 21. Relationship between standing crop and BA_5 , by classes of age: 0-5 years, filled circles; 6-10 years, crosses; 11-15 years, open circles. Hamra and Garpenberg.

Figure 22. For the material in Fig. 21, relationship between standing crop and BA_5 by age classes, mean values; relationship between standing crop and age, mean values; relationship between BA_5 and age, mean values.



1.26 Relationship between performance and age

It has been observed, e.g. by Lindman (1914), that the length of the shoots formed in any year decreases as the bush grows older, see Fig. 35. At the same time, the absolute number of shoots tends to increase, see Fig. 42. The decrease in shoot length may depend in part on a transition from mainly vegetative shoots in the basal part of the axis, to mainly flowering shoots in the upper (see Introduction). Zlobin (1961) recognised that flowering is not fully established before about the fifth year at the earliest, although this might vary from site to site. After the fifth year the upper part of the axis is dominated by flowering shoots, while vegetative shoots continue to arise from dormant basal buds.

Extension growth made during the first season by tillers arising from the rhizome may largely depend on the time of emergence, but also on the location and type of bud. Tillers which emerge in spring from rhizome apical buds which have undergone reorganisation in the previous year may make considerable growth. Often, however, incipient tillers appear to spend more than one growing season in the litter or moss layer. Figure 23 shows a series of tillers at various stages of development; see section 3.14 for further discussion. Subsequent (vegetative) growth may be rapid, but once "canopy level" has been reached in a dense stand, flowering shoots begin to dominate. The factors controlling this require further study.

Thus the first one or two years' extension growth may not be great, but are usually followed by an expansion phase (see section 3.14) of vegetative shoot production in which both average shoot length and number of shoots is greater. Thereafter, the average length of the shoots formed on an axis decreases successively. It should, however, be pointed out here that new shoots arising from dormant buds on the base of an axis which is moribund are usually of similar length to those found in the vegetative expansion phase of a new tiller.

The problem here is to discover what effect this has on the population of current shoots on a quadrat. The age structure of the population of tillers is complex, in consequence partly of an overlap of rhizome units. The effect of this may be to obscure any supposed differences in the length of current shoots on quadrats with young and old tillers. A further complicating factor is the effect of long basal shoots on older bushes, mentioned above. The primary pattern of shoot length to be expected on the tillering part of the rhizome is that of a gradual increase in average current shoot length from the young to the middle-aged tillers, followed by a decline.

Shoot length, however, may depend as much on the growth environment at any point as on the age of the tiller. There is evidence that the micro-environment in the outermost part of the stand differs from that in the closed stand, and it is not impossible that even in the latter there should be differences. Intrinsic (scilicet: age-associated variat-

ion) may be obscured or accentuated by environmental differences. Performance has previously been used as a measure of the relative vigour of plants, e.g. by Kershaw (1962), Watt (1947). It is defined here as the product of the interaction of environment and intrinsic vigour. It is expected that the longest current shoots on a quadrat should provide a measure of the performance of the tillers at that point. Strictly, however, only quadrats in the closed stand may be comparable in this respect, although performance may give useful indications as to environmental differences between the closed and the peripheral parts of the stand.

1.261 Variation in length of current long shoots

All current shoots not less than one-third of the length of the longest shoot on any quadrat were arbitrarily deemed to be long, whether or not they bore the basal spur indicating flowering. The distribution by length was similar on all quadrats, although numbers of shoots varied from one quadrat to another. Rather few shoots were greatly longer than the average, although those that were amongst the ten longest were substantially longer than the average, e.g. in H/III, where the overall average was 49.6 mm and the longest shoot 150 mm. The length of the ten longest shoots tended to increase as the total length of shoots on a quadrat increased.

1.262 Relationship between shoot length and age

Figure 24 shows the total length of the ten longest shoots on each quadrat plotted against maximum tiller age. Average values are also shown. The average length of the longest shoots increased up to an age of eight or nine years, after which it remained rather constant. The decreasing trend typical of individual axes or bushes is absent.

The maximum age of the tillers in this material was 15 years. In view of the fact that tillers may live considerably longer, it might be considered that the full age range has not been covered and therefore, that Fig. 24 has been truncated. Other studies of performance, in which age was included, e.g. Kershaw's study of *Alchemilla* (1960), covered the full age range of individuals, although population-based measures of performance have been used with success, e.g. Kershaw (1962), Watt (1947). On the other hand, it seems probable that the maximum ages encountered at Hamra and Garpenberg may be effectively the maximum ages characteristic of these sites, in which case the above objection is unlikely to be valid. Another possibility is that the apparent increase in shoot length depends on a transition from the peripheral to the closed stand, i.e. that it is an effect mainly of environment. However, by no means all the quadrats in the younger age range were peripheral. Evidence presented below also shows that in the closed stand, there were considerable differences in shoot length.

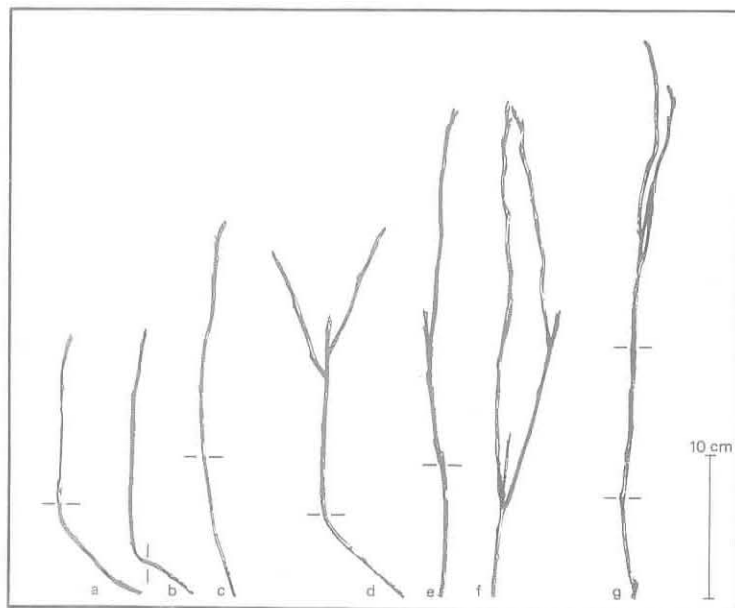


Figure 23. Tiller development and branching at Cammachmore. (a) is an orthotropic shoot shortly after reaching the surface—the tip has turned green, (b) at a later stage, (c) an emergent tiller two years old, (d-g) branching types. The lines show annual increments. Note shoot length.

Figure 25. Progression of the length of the ten longest shoots on each quadrat, H/II, G/III, IV. (Right).

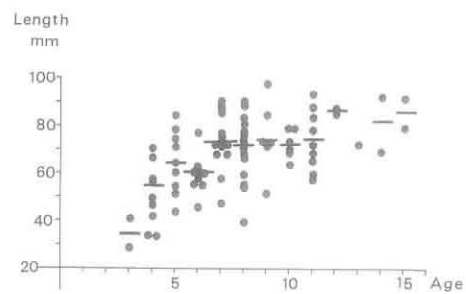
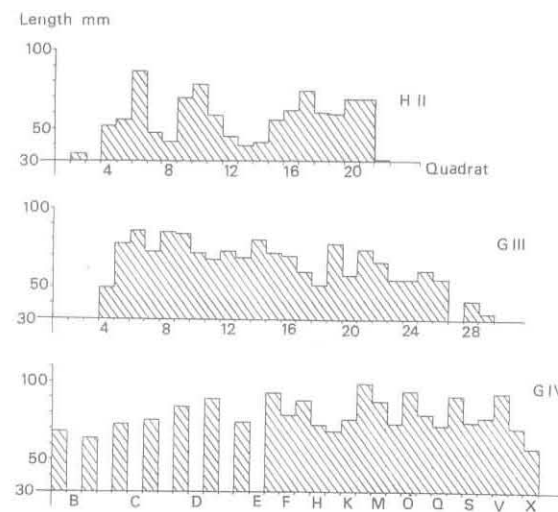


Figure 24. Mean length of 10 longest shoots on each quadrat on maximum age, and average for each age (horizontal line).

32



1.263 Progression of shoot length

Figure 25 shows the average length of the ten longest shoots plotted against quadrat position. The variations in shoot length take the form of a series of peaks and troughs, some of which are rather regularly spaced, e.g. in G/IV. However, the regularity is insufficiently pronounced and the differences too small, for definite conclusions to be drawn. If, however, the premisses outlined above are valid, it is likely that the peaks of shoot length represent some form of regeneration, but whether of young tillers or basal shoots on older bushes, it is impossible to decide. The apparent regularity may be due to chance alone. When these sequences are considered together with others, e.g. total number of shoots, number of fruits on a quadrat, it is clear that they are intimately related to some underlying sequence rather than to chance. The only sequence to which it is likely that they are related is the age sequence along the rhizome.

1.3 Stand structure and growth rate

1.30 Introduction

In the foregoing sections, evidence has been presented to show that the variation in space of standing crop aboveground— and by extension, leaf and shoot production— basal area, tentatively performance, and rhizome standing crop, is associated with the age sequence above and below ground. It remains to deduce from this evidence the structure of the stand.

1.31 Résumé of evidence

In the peripheral parts of the stand, rhizome growth is clearly centrifugal, and the primary orientation of the rhizome is also centrifugal. Rhizome age increases inwards from the periphery to age maxima which coincide with the end of the rhizome. The disposition of these points is consistent with centrifugal growth. Characteristics, such as basal area, standing crop, production of leaf and shoot, and rhizome standing crop, which are correlated with age, vary in relation to the age sequence.

There is evidence that several units of rhizome succeed one another, each overlapping its predecessor. Each such unit must be associated with a sequence of aerial shoots on its distal end. If the pattern of shoot length reflects a sequence of tiller age, the two may be

identical.

The concept of a succession of tiller sequences is not new. Earlier writers, cited by Zlobin (1961), were fully aware of the complex structure of the stand of tillers. Avdoshenko (1949) has used the term "kurtina" — "screens" to describe the arrangement of the tillers; Dengler (1944) also refers to the stands in similar terms. The structure referred to by these authors is consistent with centrifugal growth, and Zlobin's interpretation of the phases of development in bilberry "clones" depends on it. The disposition of the sequences in the stand, however, depends on the rate of rhizome growth and in the following section, this is considered.

1.32 Rhizome growth rate

If the rhizome extending from the periphery of the stand to the first age maximum (and rhizome end) encountered in the stand is a single unit, it should be possible to calculate the rate of rhizome growth. In G/III, the first age maxima encountered are 200 and 150 cm, respectively, from the margin, and are 26 and 23 years. The growth rates are therefore 7.7 and 6.5 cm per annum, respectively. In G/IV, because of the sampling layout, only one maximum is clearly visible, viz. 28 years and 200 cm, giving an annual rate of 7.1 cm. Since these figures agree amongst themselves and with other available figures (e.g. Ritchie 1955a "5 - 10 cm", Keso 1908 — see Introduction — 8.7 and 11.2 cm, Everett 1967 — allowing for delay in rhizome inception — 12.6 cm, referring to the longest rhizome), it may be possible to conclude that age maxima which are so situated that the rhizome growth rate calculated with their help does not agree with the above figures, refer to another rhizome unit.

Some error is involved in these calculations. In the first place, the rhizome age may have been wrongly determined, although the margin of error is probably of the order of ca 2 years (see Appdx I). In the second place, the exact length of the rhizome is not known, but only the number of quadrats. The error involved here is of the order of ca 25 cm — one quadrat. In general, it may be said that rhizome age is more likely to be underestimated than overestimated, while rhizome length will be as often overestimated as underestimated (the straight-line length of the rhizome is used in these calculations, the actual length being difficult to measure with the sampling system employed here). Given an approximate maximum age of 30 years and an annual growth rate of ca 7.1 cm, the expected position of an age maximum can be calculated. Thus in the interrupted quadrats of G/IV, the first rhizome should have its end between quadrats C 2 and D 1, i. e. within an interval of 75 cm. Since this was not excavated, the assumption in this case must remain untested. However, when applied to the second rhizome unit in G/III, good agreement is obtained.

It is not impossible that there should be differences in rhizome growth rate between the outermost and inner rhizome units, since

the latter are growing in an environment already occupied by a considerable length of rhizome. As Anderson (1961) demonstrated, the scale of "normal" pattern may be modified by environmental factors such as waterlogging and its associated effects, or by trampling. It is not inconceivable that competition from the older or previously established parts of a plant might have a similar effect.

1.33 Stand age

The above discussion has a direct bearing on the age of the stand. Decay of the rhizome makes it impossible to follow physically the growth of a rhizome unit for more than about 30 years in the present case. If the growth rate calculated for the rhizome unit can be applied to the stand as a whole, the total age of the entire expanded plant can be estimated. Given a constant radial growth-rate, diameter is proportional to age. This relationship has been utilised by e.g. Ritchie (1955a), Oinonen (1967) and Whitford (1949) for assessing the age of clones.

On this assumption, the age of G/III, with a diameter of ca 700 cm, is about 50 years, while that of G/IV, with a diameter of ca 1000 cm, is about 70 years. For the Hamra stands a growth-rate of the same order can be calculated, which would indicate that the age of H/II, with a diameter of 600 cm, is about 40 years, while that of H/III, of size similar to G/III, is about 50 years old. The age of the Hamra stand is about 60 years, that at Garpenberg about 100 years; there is a fair measure of agreement with the age of the bilberry clones.

The results of the study reported in this section tend to confirm the observations of previous authors, mentioned in the Introduction, particularly those of Kozhevnikov (1937), Avdoshenko (1949) and Serebryakov (1954), reported in Zlobin (1961), amongst others.

2 Population structure and dynamics

2.0 Introduction

Evidence has been presented to show that there is a morphologically determined pattern in the bilberry stand. In this section the structure and dynamics of the tiller population are considered, using as basis the quadrat population. As was pointed out in the Introduction, it cannot be assumed that interactions between quasi individuals such as tillers take place on the same basis as those between true individuals. In the first place, the genotypic differences between competing individuals, which characterise most other populations, are absent here. Furthermore, the uptake of water and mineral nutrients may be partly common to several tillers (although these aspects of the plant have not been studied here); hence competition for them may depend to some extent on the tiller's position in the system. In the same way, seniority may partly determine access to light. As an instance of the possible effect of location, the case of the rhizome adjacent to a large root may be cited; this is considerably thicker than that on the proximal side of the root. Such roots are frequently on the older part of the rhizome, near the oldest living tillers.

In the foregoing section, the uniformity of BA_5 in the closed stand was commented upon. It is not known what relation this bears to the total basal area (BA_{tot}). Closely related to this is the problem of the growth rate of the largest stems relative to the smallest and to the rest of the population: are the largest tillers dominants, and if so, by vigour or by seniority? Again, are the smallest tillers small because suppressed, or small because young? Another problem is that of mortality in the population, both as a proportion of total numbers and in relation to position in the system (cf. Zlobin 1961). In this section an attempt is made to shed light on some of these questions.

2.1 Age structure and mortality of the five largest stems

Figure 26 summarises for each stand the age distribution of the five largest stems (cf. Fig. 28), dead stems being shown in black. The average age of the sample population is also shown, and where appropriate, the number of dead stems, expressed as a percentage of all stems in the sample. It should be noted that of the stems on the quadrats with the highest stem age, those dead are not necessarily the oldest.

Three main points emerge here. First, that the average age of the four populations differs, those at Garpenberg being the older. Secondly, that there were no dead tillers in the Hamra material. Thirdly, that the absolute number of dead stems was identical, and the percentages closely similar, in both Garpenberg stands.

In the two Garpenberg stands, the absolute numbers of dead stems differed very little from one age to another, but when expressed as a percentage of all stems in the age classes 1 - 5, 6 - 10, 11 - 15 years, the proportion of dead stems increased with age (see Tab. 2).

Age	C	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Age class			1					2					3		
No.	0	1	11	19	47	47	28	30	26	8	13	5	2	1	3
Dead	0	0	0	1	1	2	3	3	3	0	3	0	0	1	1
%		2/78	2.6 %			11/139	7.9 %				5/24	20.8 %			

Table 2. Dead tillers by classes of age, G/III and IV.

The distribution of dead tillers in the Garpenberg material indicates that they could have been expected at Hamra, notwithstanding the differences in average age. It is improbable that this difference depends on bias in sampling; it suggests that there is a qualitative difference between the two samples. Agreement within each site further suggests that the difference is associated with site as such rather than with the stands. This conclusion must, however, remain tentative until more evidence is available.

It remains to be seen how the mortality of the largest stems is related to that of the remainder of the population. There are first several practical difficulties to overcome. First, it is not feasible to count annual rings on all tillers on all quadrats. The assessment must therefore be based on a subsample of quadrats. Secondly, the error involved in counting rings in dead and decayed stems is considerable. If there are many decayed stems on a quadrat, the age structure cannot be reliably established, even though the number of dead stems may be known. One way of circumventing this difficulty is to express mortality in terms of diameter-class, on the assumption that age and diameter are closely enough related for this to be acceptable. But unless the status of the small-diameter tillers is established by detailed study, this method also involves uncertainty. On balance, it gives access to a larger material and reduces some sources of error, therefore it will be employed.

2.2 Diameter class distribution

Figure 27 shows the diameter-class distribution of the five largest stems for all stands, dead stems being shown in black. The percentage of dead stems by diameter class groups is given in Tab. 3.

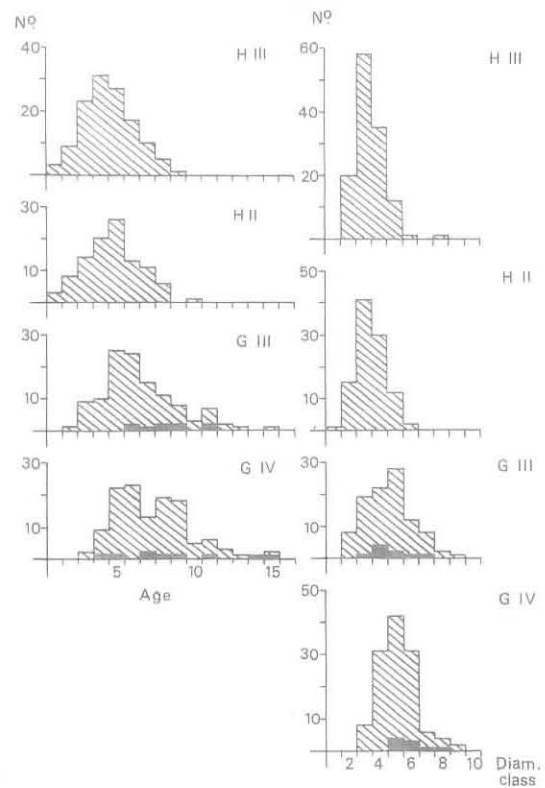


Figure 26. (Above, left), Age distribution of five largest stems, Hamra and Garpenberg. Dead stems — black.

Figure 27. (Above, right). Diameter class distribution of five largest stems in all stands. Dead stems — black. Class I 0.51-1.00 mm, 0.5 mm classes.

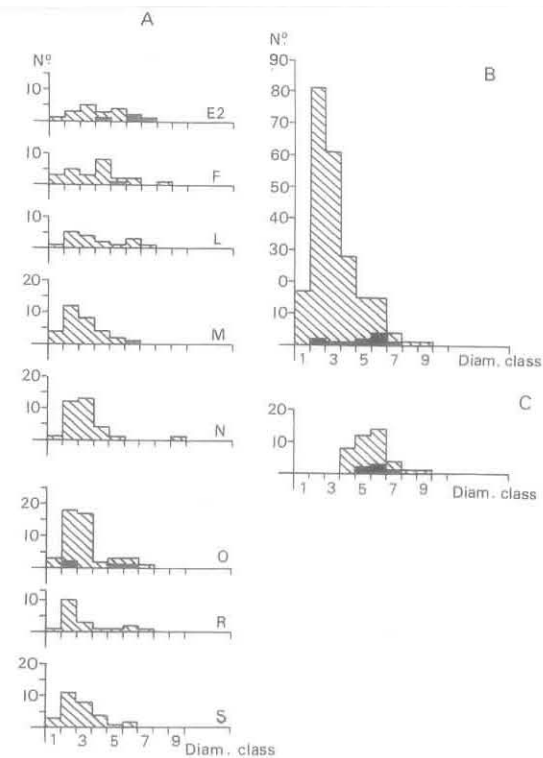


Figure 28. (A) diameter class distribution of stems in G/IV subsample, dead stems black. (B) combined diameter class distribution for subsample (0.5 mm classes). (C) diameter class distribution of five largest stems (40 in all) in subsample of G/IV.

Diam. class group	A 0.51 - 2.00 mm	B 2.01 - 3.50 mm	C 3.51 - 5.00 mm	Sum A-C
No. stems	35	166	23	224
No. dead	1	14	3	18
% dead	2.9	8.4	13.0	8.0

Table 3. Percentage of dead tillers by classes of diameter, G/III and IV.

This distribution resembles that obtained when the age classes were used as the basis. Since there were rather few dead tillers, small absolute changes produce disproportionately large effects on the percentages. Since, however, there is a fair measure of agreement, it should be permissible to use this approach, supplemented by detailed study of the age distribution on a few quadrats.

2.3 Diameter class distribution and mortality in the tiller population

Figure 28 shows for each of eight quadrats from G/IV the diameter class distribution of the whole tiller population, dead tillers being shown in black. The figure also shows the combined diameter class distribution for the eight quadrats and that for the five largest stems on these quadrats (Fig. 28 a, b and c respectively). Table 4 summarises these figures.

Material	Diam. class group, mm	A 0.51 - 2.00	B 2.01 - 3.50	C 3.51 - 5.00	Sum A-C
I. Five largest on 8 quadrats	No. stems	-	34	6	40
	No. dead	-	5	1	6
	% dead	-	14.7	16.7	15.0
II. All til- lers on 8 quadrats	No. stems	159	58	6	223
	No. dead	3	7	1	11
	% dead	1.9	12.1	16.7	4.9
III. All til- lers excl. 5 largest	No. stems	159	24	-	183
	No. dead	3	2	-	5
	% dead	1.9	8.3	-	2.7

Table 4. Mortality by diameter class groups and population categories, G/III and IV.

The table shows that the percentage mortality for the whole sub-sample population of tillers was 4.9 per cent, varying from 1.9 per cent for the smallest to 16.7 per cent for the largest. Comparison of row (I) with Tab. 3 above shows, however, that the percentage dead amongst the five largest stems was appreciably higher than in the material as a whole. This probably depends on the small total number of dead

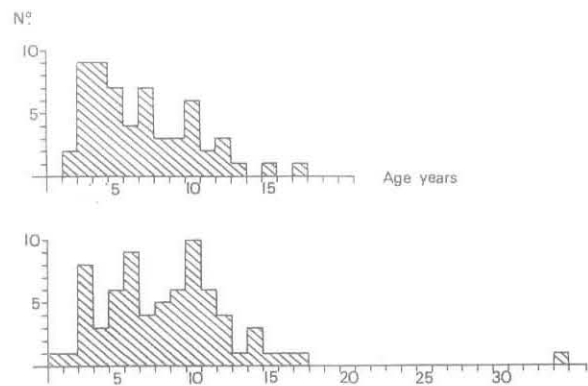


Figure 29. Age class distribution Cm I & II.

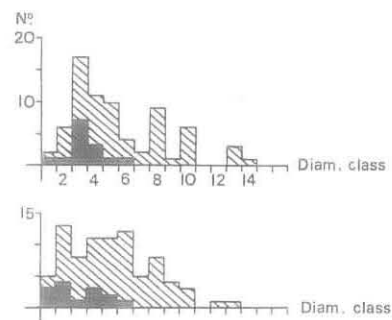


Figure 30. Diameter class distribution Cm I & II. Class 1 0.51-1.00 mm, 0.5 mm classes.

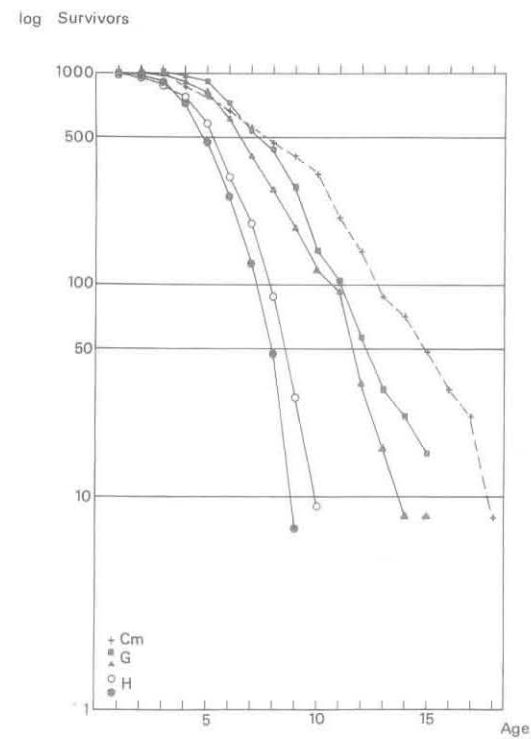


Figure 31. Age distribution curves based on an initial population of 1000, for all stands. Obtained from cumulative age distributions of Fig. 26 & 29. See text, pp 44-45, for assumptions involved. Dead tillers of indeterminate age omitted.

stems. Nevertheless, the two are of the same order. It may therefore be permissible to take row (II) as indicating the percentage distribution of dead stems in the tiller population in question. The implications of this result are discussed below.

2.4 Age analysis of two populations

The age of all tillers on two quadrats at Cammachmore was determined. The results are summarised in Fig. 29. Some tillers were too decayed for either their age or their diameter to be determined precisely; the dead tillers (black) in Fig. 30 have, however, been assigned to a diameter class which is approximately correct.

The two populations (Cm I from the outer and Cm II from the inner part of the stand) differed in their age structure, as Fig. 29 shows. The differences are further illustrated in Tab. 5 below. Quadrat II had both a larger number and a higher percentage of middle-aged and old tillers than quadrat I; the 34 year old tiller is unusual, both because it was twice the age of the next oldest tiller and because it was still vigorous. The difference between the two quadrats in respect of age structure seems otherwise consistent with their relative position in the stand.

Quadrat No.	0 - 6		Age class 7 - 12		Over 12		Total
	No.	%	No.	%	No.	%	
I	31	53.4	24	41.3	3	5.1	58
II	28	39.4	35	49.2	8	11.2	71

Table 5. Age distribution by age-class groups, Cm I and II.

Figure 30 also illustrates another noteworthy difference between these quadrats and those from Garpenberg. Whereas in the latter the percentage of dead tillers increased with diameter (*scil.* age), at Cammachmore none of the older tillers was dead; all dead tillers were of small diameter. Dead tillers made up 19.4 and 17.1 per cent, respectively, of all tillers on the two quadrats (cf. Tab. 4). Table 5, however, does not take into account the dead tillers which could not be aged precisely. The microscopic examination which could be made on them suggested that they were generally not more than six years old. They should therefore be included in the first column, with the result that the percentage distribution changes, giving for Cm I 62.5 per cent and for Cm II 47.5 per cent of tillers less than seven years old. Slight corresponding changes occur in the other figures in consequence of this.

2.5 Ingrowth and mortality

The age distribution of the populations expresses the situation at the time of sampling, i.e. it shows only tillers which survived to sampling. The number of tillers in an annual class is therefore a net term. The Garpenberg material suggested that losses tended to be constant from one diameter (scil. age) class to another, in absolute terms. In the Cammachmore material losses seemed to be concentrated to the smaller (younger) tillers. Table 6 summarises information for the G/IV subsample and the Cammachmore quadrats.

Quadrat	No. tillers	BA ₅ Tot.	mm ² Avr.	BA other tillers	BA _{tot}	BA avr. 1)	Max. age	No. dead
E2	18	49	9.8	35	84	4.7] 3.6]	15	4
F	24	55	11.0	49	104	4.3] 3.4]	10	1
L	17	52	10.4	25	77	4.5] 3.4]	9	0
M	31	43	8.6	45	88	2.8] 2.1]	11	1
N	32	46	9.2	51	97	3.0] 2.3]	13	0
O	47	54	10.8	87	141	3.0] 2.5]	11	4
R	19	47	9.4	23	70	3.7] 2.7]	8	0
S	34	45	9.0	48	93	2.7] 2.0]	10	0
Cm I	72	150	30.0	452	602	8.3	17	14
Cm II	82	111	22.2	482	593	7.2	34 (17)	14

Table 6. Summary of information for subsample of eight quadrats of G/IV and Cm I and II. Note 1) : the lower of the two figures refers to the basal area of the stem of mean diameter, not shown for Cm I and II. Figures referring to BA₅ are under bark.

The table shows that there were almost twice as many tillers on Cm I and II as on the most densely stocked quadrat in G/IV and over four times as many as on the least densely stocked quadrat. This suggests that competition—primarily for light—under the tall, dense stand at Cammachmore may be intense, which may be a reason for the failure of the younger tillers to survive. Figure 29 shows an almost complete absence of one and two year old tillers for 1969, i.e. ingrowth in 1968 and 1969 was apparently nil. However, since orthotropic shoots from the rhizome may spend the first one or two growing seasons in the moss or litter layer (especially if it is luxuriant) this may be more apparent than real. Hence measurable tillers (those extending above the moss) are likely to be at least two years old. Extension growth is thereafter rapid, taking the tillers

into the canopy of the stand. Tillers which do not reach the canopy by their third or fourth growing season may decline in vigour and shortly die. One reason for a tiller's lack of vigour may be its origin. Bud location and type seem to play a part in determining the vigour of tillers which arise from them, cf. Trevett (1959, p.27). In addition, the situation of tillers under a dense canopy may be analogous to that of shaded lower branches of trees. However, the cause of suppression in tiller stands is probably to be sought in the complex interplay between factors such as those above and the physiological systems involved in e.g. the movement of nutrients in the system. Further study of these problems is clearly required.

Figure 29 shows that the number of tillers in any annual class which survived to sampling in 1969 varied rather greatly, at least in relation to the total numbers involved. At least three factors must be considered here : first, mortality, i.e. the difference between the observed number of tillers in any annual class and the number present initially; secondly, year of origin, i.e. differences between years in respect of the number of tillers arising; thirdly, possible long-term changes in the production of tillers by the rhizome. For the third of these at least, there was no evidence in the populations studied in detail.

As was mentioned above, there were indications from the Garpenberg populations that the death of tillers tended to occur with fairly constant frequency throughout the population. In the Cammachmore material, deaths were concentrated to the smaller (younger) tillers. The expectation is that they should also occur amongst the older. There was no direct evidence of this. On the assumption that death is an event that occurs with constant frequency in the tiller population, the number of deaths each year may be expressed thus:

$$\frac{\text{Number of tillers in year 0} - \text{Number in year n}}{\text{period in years}}$$

when year 0 is age 3 and year n is age 17. Therefore, in the case of Cm I,

$$\frac{(9 - 1)}{(17-3)} = \frac{8}{14} = 0.57, \text{ i.e. in round}$$

terms, four tillers will die during a period of seven years. In the case of Cm II, there are difficulties. In the first place, the age distribution is different, there being a large number of tillers in the tenth age class and one tiller aged 34 years. (It is unlikely that the age of this tiller has been over-estimated — see Appdx I). The next tiller in age is 17 years old. By the above method, two distinct rates of mortality can be obtained:

$$\frac{(8 - 1)}{(34-3)} = \frac{7}{31} = 0.23 \text{ approximately.}$$

Also, ignoring the 34 year old tiller, mortality is found to be 0.50.

If deaths occur with constant frequency, it follows that the number of tillers surviving to a given age is proportional to the number initially present in that annual class. Therefore, an estimate may be obtained of the initial ingrowth to any class by multiplying the length of the period by the mortality quotient and adding the product to the number of tillers present in year n . This might be compared with the net annual ingrowth obtained by dividing the total "measurable" tillers by the period (0 to n years). Thus in Cm I, there were 56 living tillers in 14 annual classes, making a net annual ingrowth of four tillers. By applying the same criteria to Cm II, a total of $(69/14)$ or ca five tillers a year, is obtained. If, however, the full period of $(34 - 3)$, 31 years is used, the ingrowth is reduced to ca two tillers a year. None of these figures bears much relation to the observed number of tillers in the younger age classes.

Applying the above correction to Cm II in age classes 17 (one tiller), 12 (four tillers) and 6 (nine tillers), the following estimates are obtained: (14×0.57) gives 7.98 (ca 8), (9×0.57) gives 5.13 (ca 5), (3×0.57) gives 1.71 (ca 2), therefore the estimated original ingrowth in these age classes was $(1 + 8)$, $(4 + 5)$, $(9 + 2)$.

It is, however, quite clear that this correction depends on the arbitrary assumption of a linear mortality rate and on the exclusion of the 34 year old tiller. But the correction does give an estimate of the annual ingrowth which agrees closely with the observed numbers in the younger age classes. In Cm I, the number of tillers calculated for age classes (3 - 17) was 115, giving an ingrowth of ca eight tillers a year. The variations in numbers in annual classes remain unexplained; they may be chance or be associated with environmental variations, i.e. "good" or "bad" years. The problem of mortality—and its other aspect, survival—is further discussed below.

2.6 Survival

Ingrowth and mortality are only one side of the coin; the other is survival. Figure 31 shows for the combined populations of Cm I and II and those from Hamra and Garpenberg, survivorship curves (survivors per thousand arising; cf. Odum 1959, p. 164 ff.). According to Odum, a diagonal straight line is characteristic of a constant specific mortality rate, while a convex curve characterises a population which lives out its inherited lifespan, all individuals dying within a short time.

The curves shown here do not follow this ideal form for constant specific mortality, neither do they exhibit the extremely convex form. However, once past the early stages of life, all five populations had an almost constant rate of decline. The two Hamra populations were closely similar, the two Garpenberg populations were distinct from them but resembled each other, while the joint Cammachmore population was distinct from those at Garpenberg. It should be noted that the 28 tillers which died before the age of seven years were not in-

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cluded in the Cammachmore population, although their inclusion does not markedly alter the course of the curve. The assumption of a constant mortality rate is not strictly correct; but the lower portion of the curves deviates little from linearity.

If these populations are to be employed in studies of mortality rate, certain conditions must be fulfilled. First, the age of the oldest tillers encountered must reflect the longevity of tillers in the population from which the sample is drawn. The close similarity of structure of all the sample populations studied makes it probable that this condition is fulfilled. Secondly, the age class distribution of the tillers in the sample must bear some relation to that in the population at large, i.e. the decrease in numbers from one age interval to the next in the sample should parallel that in the population from which it is drawn. Thus of 1000 tillers which form the initial population, some will die in the interval between one age class and the next until the maximum age is attained, when none of the original tillers remains. However, in the Cammachmore populations, in spite of the almost complete reduction of the original population by age 18 years, the presence of a 34 year old tiller indicates that tillers which survive to age 18 years have a good chance of living substantially longer. The 34 year old tiller was still vigorous and would probably have lived several years longer.

The maximum age differed between the three sites studied, but showed internal similarities. Another, and perhaps more useful measure of the lifespan of tillers, is their half-life (cf. Harper 1967), i.e. the length of time during which half of the original population dies. For H/III, this was ca 4.8 years, for H/II ca 5.5 years, for G/III ca 6.5 years, for G/IV ca 7.3 years, and for the uncorrected Cammachmore populations, ca 7.7 years. In comparison with the half-life of the individuals of *Sanicula europaea*, *Filipendula vulgaris* and *Centaurea jacea* studied by Tamm (1956) and recalculated by Harper (1967), the half-life of the tillers in the bilberry populations studied here was very short. Failure to observe deaths amongst the very youngest individuals has probably resulted in an overestimate of the half-life for all five populations.

In Tab. 4, figures are given for the mortality of various classes of tiller in the Garpenberg subsample. Strictly speaking, these figures refer to the percentage of standing dead tillers at the time of sampling. It has already been pointed out that there were no dead tillers at Hamra, contrary to expectation. It may be that no dead tillers were amongst the five largest stems on any of the quadrats; this seems improbable. If the number of dead tillers in a stand at any moment is related to the mortality rate, then with the short lifespan and apparently high mortality rate, there should have been some dead tillers. If, however, the rate of breakdown of a dead tiller is higher in one population than in another, and both have a similar mortality rate, then fewer standing dead tillers would be encountered in the population with the higher decay rate. The differences between Garpenberg and Cammachmore in respect of percentage standing dead suggest that this point should be followed up; for clearly, differences in decay rate have some bearing on the relative rates of turnover on the sites in question.

2.7 Stand density, basal area and age

The figures in Tab. 6 suggest that the average basal area of tillers decreases as the number of tillers on a quadrat increases. This is analogous to the situation in forest stands. It is here expected that the relationship will take the form of an hyperbola, the value of the horizontal asymptote being equivalent to the basal area of the orthotropic shoot, this being a "morphological constant". It is clearly difficult to compare the relationship between basal area and stand density in the Cammachmore material with that for Garpenberg, as only two quadrats are available for Cammachmore. Nevertheless, it can be concluded that they do not lie on the curve for the Garpenberg material.

Stocking density increases from the outer to the inner part of the stand (e.g. H/III), i.e. with the age of the system. In relatively young stands, density will be clearly zoned. In older stands, in consequence of "filling-in", stocking density will increase; Zlobin's (1961) conclusions suggest that after the tillers reach a certain age, stocking density may well decrease.

It has been shown that BA_5 is correlated with the age of the oldest tiller on a quadrat. There are also indications that basal area may be characteristic of a site. In other words, once stocking density reaches the level at which the site is fully occupied, there will be no increase in BA_{tot} for an increase in the number of stems, although fluctuations will occur. The relative constancy of BA_5 in the closed stand has already been commented upon. Table 6 shows that for the Garpenberg subsample, no constant relationship between BA_5 and BA_{tot} can be deduced; but this material is admittedly meagre. The question is this: Which of these two measures better expresses the productive capacity of the site? If, as it seems, BA_5 is largely independent of density, then it should be a better defined measure of productive capacity than BA_{tot} , which up to the threshold of full stocking must be dependent on density.

Full stocking in itself may be an elusive concept, since there are indications that it may be as characteristic of site as e.g. basal area or longevity. Thus comparison between sites on the basis of adjustment to a common density of stocking may be misleading.

2.8 Résumé

In the introduction to this section, some of the problems involved in population studies in bilberry stands were outlined. The results of these studies are briefly summarised here.

The five largest stems on a quadrat appear to be dominants, partly

by seniority and partly by vigour (cf. Fig. 18, 53). Tillers amongst the five largest stems generally grew up under conditions of stocking density similar to those under which the youngest tillers now exist. Most of the tillers of small diameter are young; but if those which arose in the same year are compared (see Fig. 18, 53) it is apparent that the range of basal area is considerable, even on the same quadrat. Examination of the course of radial increment gives no unequivocal explanation of the differences. Some tillers had a large initial diameter, which may depend on bud type or consequently, on length, with all that this implies (see section 3), and maintained their lead throughout life. Other tillers had closely similar initial basal areas, but soon diverged, while yet other had a similar course of growth, but finally diverged. Most of the tillers which had a large final diameter or basal area tended to have grown fast during the first four growing seasons. The part played by their bud type and location was not studied here, but might provide an insight into the causes of the differences found (cf. Trevett 1959).

The frequency and distribution of standing dead tillers varied considerably between the stands studied. In the Garpenberg stands, dead tillers tended to occur throughout the population, but were infrequent amongst the youngest. At Cammachmore the situation was reversed. No dead tillers were found amongst the five largest stems at Hamra. The mortality rates and half-life of the five populations studied differed, as did also their longevity.

3 Growth and variation in the aerial shoots

3.1 Long shoots

3.10 Introduction

The division of function between vegetative and flowering shoots was outlined in the Introduction, and some indication was given of sources of variation. Some of these are discussed in greater detail later. It has been observed that there is a gradual decrease in shoot length and leaf size with increasing age, while the absolute number of shoots tends to increase. Part of this process is associated with ageing as such, and its effect on the growth of the tiller is considered here.

3.11 Relationship between shoot length and diameter

In addition to the increase in the number of shoots formed each year, there is an increase in the diameter of those formed earlier. It is inconvenient to measure this increase on TS and for the present purpose, unsuitable; the increase in diameter must therefore be expressed indirectly. Both weight and length can be measured accurately; weight divided by length gives a quotient, weight per unit length (q). Increases in this, length being constant, will correspond to increases in diameter. For structural reasons long shoots are expected to be of greater diameter than short, i.e. diameter is in some way proportional to length. This may after some years constitute a source of error in calculations of increment and must therefore be studied.

Figure 32 shows the weight of individual current (C) shoots plotted against their length, for material from Hamra and Garpenberg. The relationship is curvilinear, implying that diameter increases with length. Scattering increases with length. Figure 33 shows for the same material, q plotted against length. The value of q appears to increase linearly on length, but the variation is considerable. Table 7a shows for 10-mm classes of length the average value of q in current shoots up to 100 mm long. The values for shoots over 80 mm long are anomalous; in Tab. 7b, for the C + 1 shoots, there is a similar anomaly. Expectation is that they should lie on a straight line. The values of q for shoots longer than ca 70 mm suggest that there may be a fundamental difference between long shoots and short in respect of their subsequent diameter growth. This is discussed below.

3.12 Weight increment

Figure 34 illustrates the increase in q from C shoots to C + 1 and C + 2 shoots in the material from "Skogshögskolan". The figure shows that the C shoots were relatively closely clustered, although scattering tended to increase among the longer of them. The C + 1 values differed little from those for the C shoots; the anomalous value for a short shoot prob-

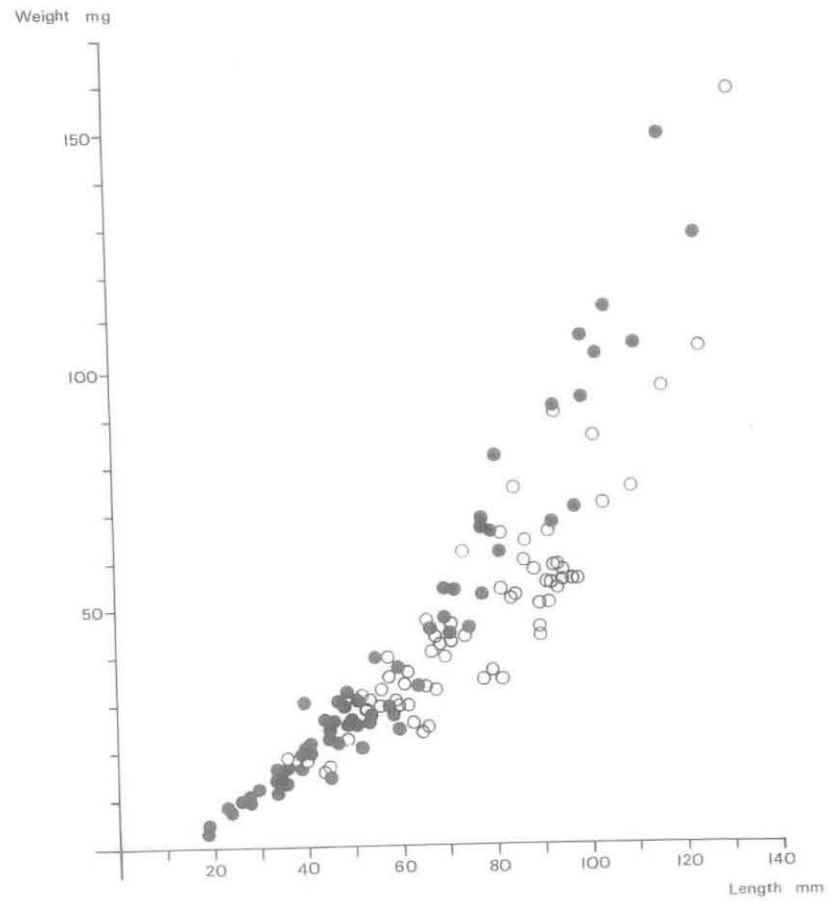


Figure 32. Weight of current shoots against their length, for material from Hamra (filled circles) and Garpenberg (open circles). Values of q for the material are shown in Fig. 33.

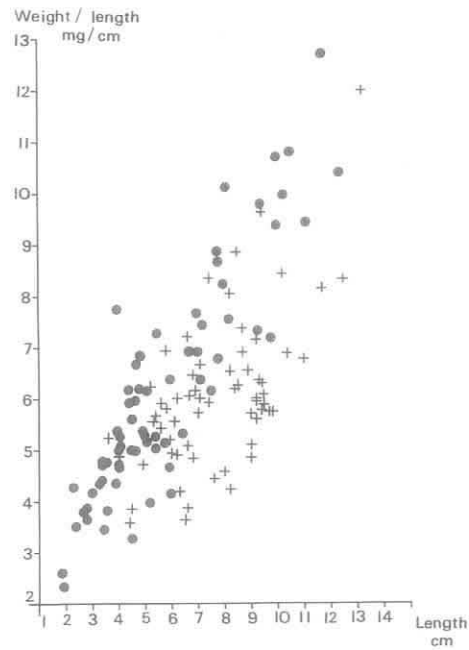
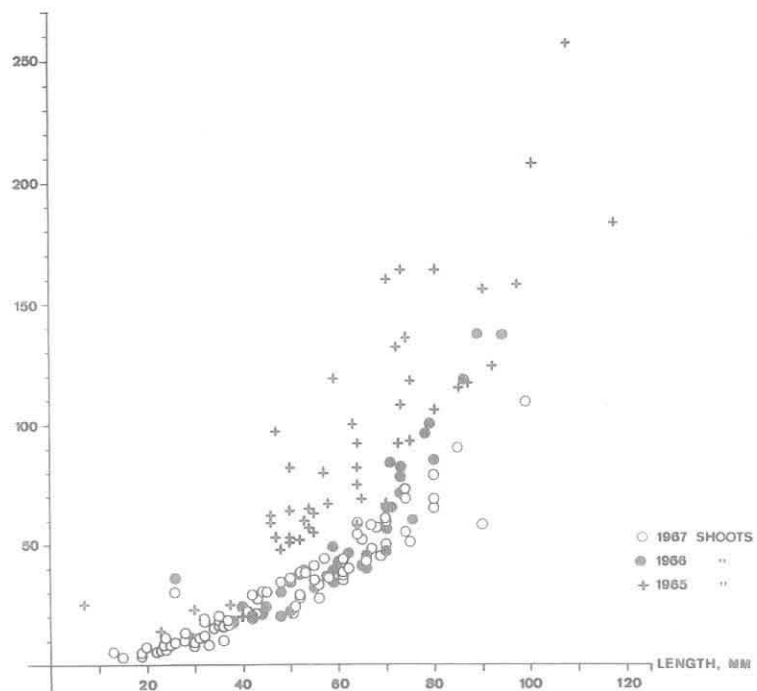


Figure 33. Values of q for the material of Fig. 32, against length. Filled circles Hamra, crosses Garpenberg. Note differences in dispersion.

Figure 34 (below). Shoot weight against length for C (1967), C+1 (1966) and C+2 (1965) shoots, Skogshögskolan. Observe increase in weight with age, and increased dispersion.

SHOOT WEIGHT,
MG



Length class mm	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
A) W/L mg/cm								
q_C	3.8	4.8	5.1	5.5	5.7	6.8	6.6	6.5
Average under & over 70 mm			5.3				6.7	
B) W/L mg/cm								
q_{C+1}	-	5.5	6.0	6.8	7.2	9.8	10.5	10.6
Average under & over 70 mm			6.7				10.2	

Table 7 a, b. (a) Weight per unit length by classes of length, current shoots Hamra and Garpenberg.
(b) Weight per unit length by classes of length, C+1 shoots from Hamra, Garpenberg, Skogshögskolan.
Averages for shoots greater and less than 70 mm.

Year	C		C+1		C+2		C+3	C+4	C+5
Length class mm	<70	>70	<70	>70	<70	>70	all	all	all
mg/cm	5.8	7.1	6.6	10.3	10.4	14.2	14.1	32.7	53.5
All		6.3		8.2		11.0			

Table 8. Weight per unit length by classes of length for shoots up to six years old.

ably resulted from the inclusion of a truncated long shoot. However, the longer of the $C + 1$ shoots merged into the lower ranges of the $C + 2$ shoots. The value of q for the latter was considerably more variable than those of the younger shoots over the same interval of shoot length, and in still older shoots ($C + 3$ and older) the scatter increased still further.

Since the material was collected at random, the variation in q for any particular shoot cannot be ascribed to a specific source. There is, however, a relationship between shoot length and number of leaves, therefore with the number of buds. Even though no more than half of the buds on a shoot give rise to new shoots in the following year, the longer is the shoot, the greater is the potential production of new shoots. (See section 3.14). There is also a relationship between the length of a shoot and the length of the shoots which arise from it, i. e. although average shoot length decreases with age, long shoots tend to give rise to relatively long shoots (see Fig. 35). Therefore a shoot which is long initially will probably acquire an assimilating superstructure larger than that developed on a shorter shoot (see Fig. 36). The reduction of the number of buds by shoot formation in the year in which the bud is laid down (prolepsis), the effects of shading and crowding, etc., may obscure this to some extent, but it is nevertheless likely that shoots which are initially long will have greater diameter growth than those which are short, for some years at least.

If this reasoning is valid, much of the scatter of q values in shoots older than two years could be reduced by classifying shoots according to the assimilating superstructure developed on them, see Fig. 37.

Table 8 shows the course of increase in q for shoots up to six years old. Shoots older than this, because of the formation of cork, which obliterates their angles (cf. Grevillius & Kirchner 1923, Bright 1928), tend to resemble the terete base and were therefore investigated on TS.

3.13 Diameter growth

In Fig. 18 the average diameter growth of the five largest stems from Hamra and Garpenberg was shown, also that of the tiller populations from Cammachmore. Figures 38, 39 and 40 are the scatter diagrams of diameter on age on which the averages are based. There is wide variation in the diameter at any age, although the material from Hamra is somewhat more compact than the others.

For closer study of diameter increment, the material from Cammachmore was used. Diameter over and under bark, and ring width, were measured with the help of a projecting microscope.

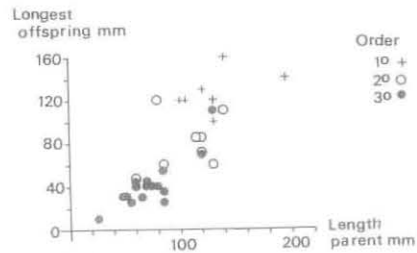


Figure 35. Relationship between length of parent shoot and length of longest offspring, for three orders of shoot.

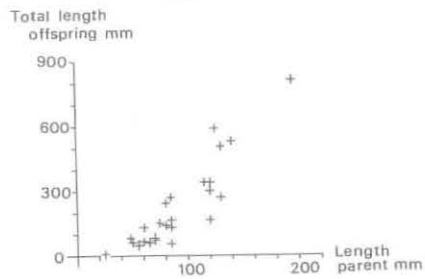


Figure 36. Relationship between length of parent shoot and total length of all shoots arising from it.

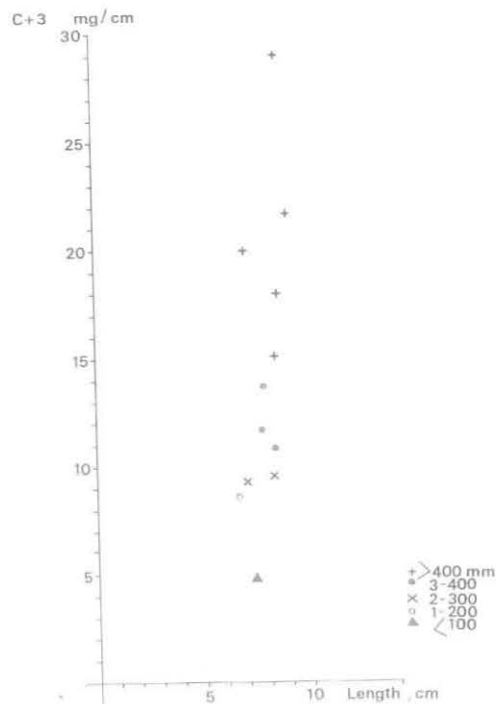


Figure 37. Distribution of q for C+3 shoots of similar initial length, by classes of length of offspring. The q values tend to increase with increases in the total length of the superstructure of shoots on them. But compare variation in q for C shoots, Fig. 33.

Figure 41 shows annual ring series from individual tillers from Cammachmore. None is less than ten, and the oldest is 34, years old. Nos. 10-16 are tillers which originated in 1960. No. 18 is a composite annual ring series based on Nos. 1-16, while No. 17 is a life curve, showing the course of decrease in ring width with age.

The fluctuations in ring width in the older series largely coincide. In the younger, there is little coincidence, this being particularly marked amongst those from 1960. The agencies responsible for these fluctuations may be endogenous, e.g. associated with the vegetative expansion of the bush, or exogenous, e.g. associated with weather or damage.

The expansion phase of growth was mentioned above and is treated further in section 3.14. It usually begins in the fourth or fifth year, rarely earlier, sometimes later, and may affect one or several axes. It depends immediately on the availability of a large number of buds, implying long shoots in the previous year or a stimulus to dormant buds on older shoots. The extent to which environment, e.g. the weather in the year of bud formation, may influence the type of bud laid down—flowering shoot or vegetative—is not known. An internal phasing of development is known to exist (cf. Zlobin 1961), whereby the general development of flowering shoots does not begin until the fifth to eighth year.

The older ring series, both from Cammachmore and from another site west of it, suggest that some of the synchronous fluctuations, e.g. in 1959, may depend on weather conditions in the years in question (cf. Mork 1946a). However, this conclusion must remain tentative until detailed ring analyses are available (in preparation). There was no apparent connection between the large fluctuations in Nos. 9-16 and any in the older series. It is therefore tentatively concluded that the former are primarily endogenic, although the causal connection remains obscure.

Studies of the internal relationships in different parts of the same axes indicate that these may be complex. Attempts to interpret "uncorrected" ring series in bilberry are likely to be difficult, autocorrelation between ring widths and the marked decrease of ring width with age being only two of the problems involved. Preliminary observations on other dwarf shrubs suggest that the situation there is similar.

3.131 Ring width relationships

This section is based on material from a pilot sample, therefore limited treatment only of the relationship is possible. It is intended to study it further in clonal material under defined conditions.

Serial TS were cut from the basal part of 25 bushes, along each main axis to the C shoots. Each "annual" shoot increment thus sec-

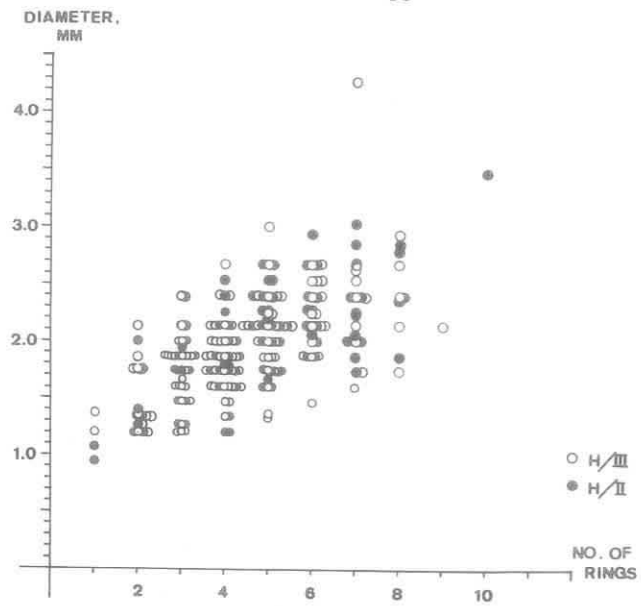


Figure 38. Scatter diagram of diameter under bark on age for five largest stems in H/II & III. Note the relative compactness of the material in any age-class, compared with Garpenberg and Cammachmore.

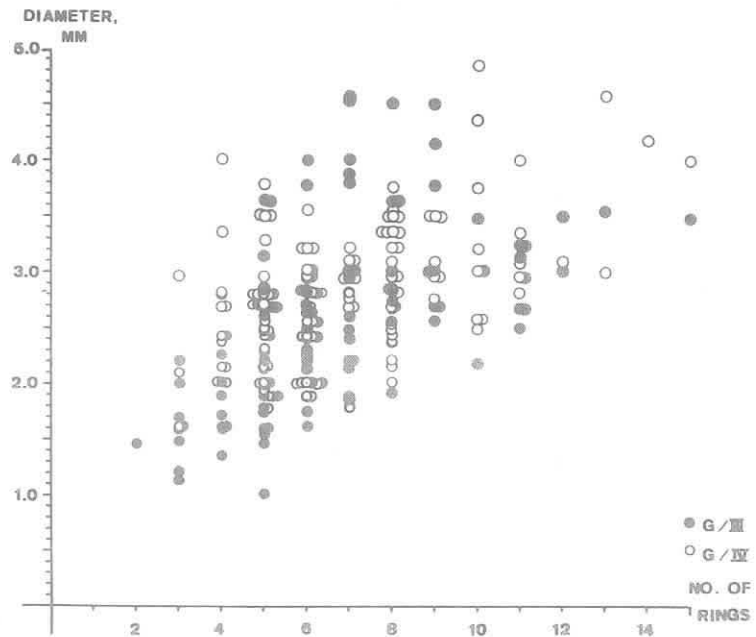


Figure 39. Scatter diagram of diameter under bark on age for five largest stems in G/III & IV. Compare with Hamra.

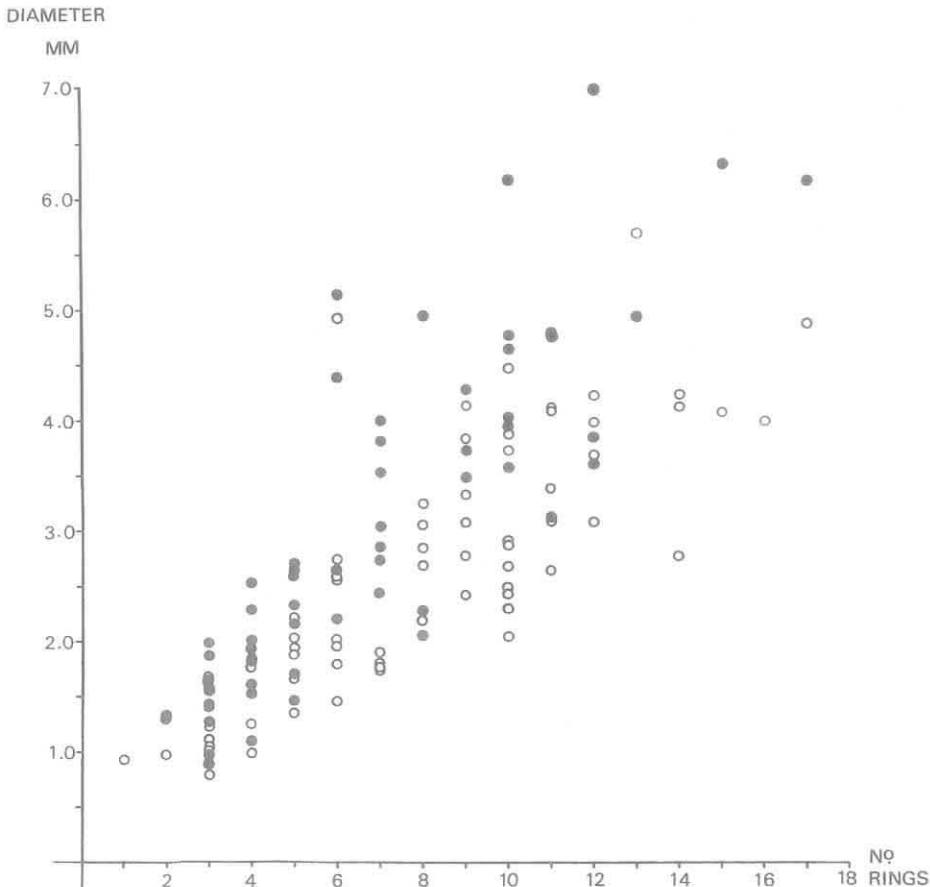


Figure 40. Scatter diagram of diameter under bark on age for Cammachmore material. Open circles Cm I, filled circles Cm II. For convenience the 34 year old stem, diam. u. b. 6.12 mm, has been omitted. Observe the range of diameter for the same age, and compare Fig. 38 and 39.

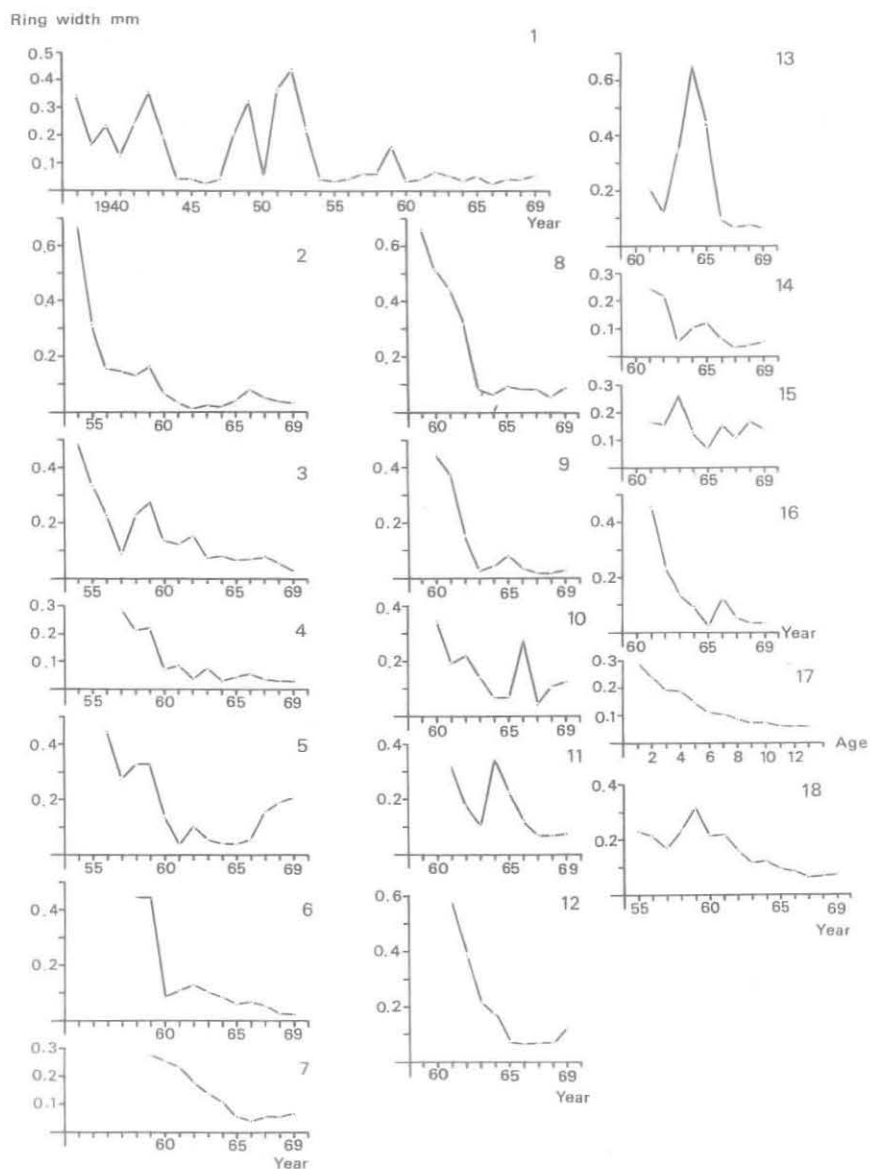


Figure 41. The eighteen diagrams here show the course of radial growth in tillers of different ages from Cammachmore. Nos. 1-16 are for individual tillers, to illustrate coincident and non-coincident ring width fluctuations. The latter are prominent amongst younger tillers, while coincident fluctuations e.g. 1959, are more noticeable amongst the older. No. 17 is a life curve for bilberry, showing decrease in average ring width with age, while No. 18 is an uncorrected annual ring series for Nos. 1-16. Cf. Mork, 1946.

tioned was measured, the total length of shoots on each axis and each bush being obtained in this way. On each of the increments forming the axis, ring widths were measured on a basal TS. The width of the rings formed in the same year at different levels in the axis was compared and an attempt made to discover the relationship between ring width and shoot growth in any year.

The study confirmed the relationship between initial shoot length and diameter and showed that as expected, the width of a ring formed in any year tended to decrease down the axis, although this was not invariably the case. It also brought out clearly the fact that attempts to determine the age of an old bush by counting back the shoot increments give unreliable results. However, it was not found possible to establish satisfactorily a relationship between ring width and shoot growth. This may depend on the inadequacy of the material or on shortcomings in the technique used (e.g. the area of wood formed in each year might be more suitable than the average ring width); but it seems likely that losses of shoots, and truncation of shoots by apical die-back, introduced considerable error. This investigation is therefore not referred to in detail here. Further study of the relationships is desirable.

3.132 Density

To integrate the increment of the shoot base with that of the upper parts of the axis, the wood density is required. To discover whether density varied with age or diameter, the density of stems of various diameters was determined by the mercury displacement method under bark (Ericson 1959). Five stem sections in each of three diameter classes were investigated. There appeared to be no difference in density between the classes, for which reason the average density of 0.5717 was used for converting diameter increment to weight per unit length (but cf. Mork 1946b, for density).

3.14 Branching

Figure 42 shows schematically the increase in the number of shoots and the decrease in average shoot length with age, in two bushes. These diagrams suggest that the number of shoots that arises each year is proportional to the number of shoots available at the beginning of the growing season, i.e. that have survived the winter. Not all buds on these shoots produce shoots in the following year, and not all the shoots are vegetative. In general, distal buds on the C shoot give rise to shoots in the year after they are laid down (excluding those which develop proleptically), while proximal buds remain dormant. Table 9 indicates that about half of the buds present in any year remain dormant. Many of the shoots which develop proleptically in late summer are flowering shoots, and may account largely for the second flowering period in the autumn (Ritchie 1955a).

These shoots seldom persist to the following year, but fall with the leaves or in the late winter.

Year	C + 1	C + 2	C + 3
Total buds	65	27	10
Dormant buds	28	16	4
% dormant	43	59	40

Table 9. Numbers of dormant buds from year to year in bilberry, Skogshögskolan.

Table 10 shows shoot length and number of buds on C long shoots from H/II, III and G/III. The averages disguise the variation in the stands, for both shoot length, number of shoots and number of buds on each quadrat follow a sequence closely similar to that of the ten longest shoots. The considerable differences both between Hamra and

Site	No. quad- rats	No. shoots		Avr. shoot length, mm	Total shoot length/quad. cm	Avr. buds	
		Tot.	Quad.			Shoot	Quad.
H/II, III	42	1832	43.6	48.0	209.6	5.81	253.8
H/II	19	520	27.3	43.1	118.1	5.55	152.1
H/III	23	1312	57.0	50.0	285.2	5.92	337.8
G/III	25	1669	66.8	44.6	298.4	5.50	367.4

Table 10. Shoot length and number of buds, on individual long shoots and by quadrats, H/II and III and G/III.

Garpenberg and between H/II and H/III are evident. The origin of the difference between the two Hamra stands is not known; it may be environmental or inherent, the latter being well known amongst North American *Vaccinium* species, clones of which on the same site exhibit large differences in growth rate, etc. (although in this case, taxonomic difficulties may also be involved, because of extensive hybridisation). Further study of these two stands is in progress.

If only the vegetative shoots, defined by the criteria used here (Appdx I), are considered, the course of growth in a bush during the first few years can be approximated. If the number of shoots in any year is V , and the number developing on them in the following year is V_1 , then approximately

$$V_1 = V \cdot k, \text{ where } k \geq 2.$$

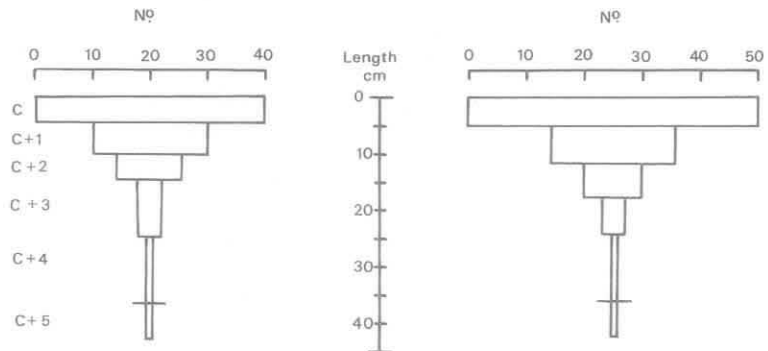


Figure 42. The course of increase in number and variation in average shoot length in successive years in two bushes. Material from Skogshögskolan.

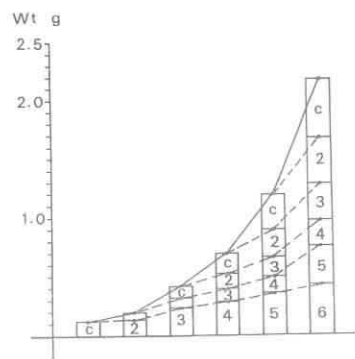


Figure 43. Diagrammatic representation of the growth model, showing weight increment over a period of six years. Based on schematic course of increase in shoot number and development of shoot length.

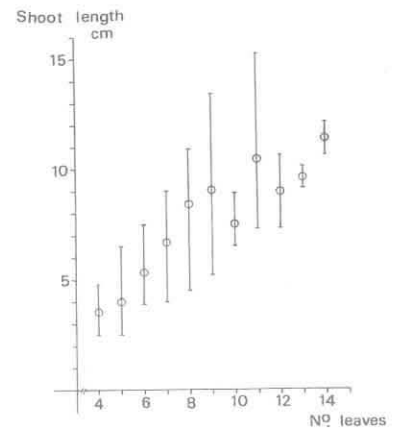


Figure 44. Relationship between number of leaves and shoot length. Bars show the range of shoot length for any number of leaves, circles show mean shoot length.

Table 11 shows for twin tillers, i. e. tillers arising from a bifurcated rhizome, the number of shoots produced in six successive years. Growth in these tillers was unusually regular. Axis C, from the same stand, had a similar development but expanded more rapidly, which probably depends on its having arisen from a basal bud on an older tiller. The last example, D, developed less regularly (although the figures are net, since shoots lost could not be accounted for) and is an example of the course of growth when secondary axes arise from dormant buds after a few years.

Sample	Year	C	C+1	C+2	C+3	C+4	C+5	C+6	C+7	C+8
Number of shoots										
A }		41	20	11	4	1	1	-	-	-
B }		50	21	10	4	1	1	-	-	-
C		31	9	3	1	-	-	-	-	-
D		82	41	28	20	11	6	1	1	1

Table 11. Number of shoots formed in successive years in four bushes. Tillers A & B twin, axis C from a basal bud, D bush with secondary axes. "Long" shoots only.

These figures indicate that there is some degree of regularity in the growth of the tiller in its earlier stages, while that of the axis developed from a basal bud is less regular and that of the bush may be irregular. Nevertheless, some conclusions may be drawn if a simplification is introduced. Figure 1, reproduced from Zlobin (1961), points the way. The bilberry bush may be considered as a system of axes, arising at different points in time, but passing through a similar development in respect of the length of the annual increments and their increase in number.

3.15 A preliminary growth model

It is now intended to show diagrammatically, for a model axis, how weight increases with age and how the increase is distributed throughout the axis. Three points should be borne in mind when this model is considered: First, that it is highly schematic. It is here assumed that the constant of increase in number is $k = 2$, and that the length of the annual shoot increments is in the relation 6 : 10 : 8 : 7 : 6 : 5 units for an axis six years old. This simplification ignores the characteristic expansion phase. Secondly, it is assumed that no flowering shoots develop during this length of time; the model considers only vegetative shoots. Thirdly, it is assumed that losses do not occur. See Fig. 43.

The purpose of this model is to provide a reference against which the growth in individual axes on different sites in nature can be compared. It is in no sense representative of any site and cannot at this stage be considered more than an approximation, from which in due course a more realistic model will be constructed. There are other

approaches to the construction of growth models, e. g. the relationship between basal area and weight in individual bushes of different age; it is intended to pursue this approach parallel with that above, in future work.

3.16 Interdependent relationships

3.161 Leaf number, leaf size and shoot length

Changes in the number of leaves per shoot accompany changes in shoot length. Figure 44 shows the relationship between shoot length and number of leaves; within the limits of the material examined, the number of leaves increased with shoot length, although, as may be seen, there was wide variation in the number of leaves for a given length of shoot. The study of internode lengths suggests that this depended partly on the time at which extension growth ceased, the distal internodes being very short in many shoots with a large number of leaves relative to their length. A small sample of shoots longer than 140 mm (such shoots being uncommon in this material) indicated that the length of internodes tended to increase, which may have been the case in the 300 mm shoots reported by Mork (1946 a).

Leaf size is related to shoot length, long shoots having larger leaves than short. To express the relationship between age, shoot length, number of leaves and leaf size, the length of leaf No. 4 (see Appdx I) was multiplied by the number of leaves per shoot and the product plotted against shoot length. Age was introduced by separating axes into those older, and those younger, than six years of age. Figure 45 confirms that current shoots on young axes tend to be longer and to have more and larger leaves, than those on older axes.

3.162 Leaf weight

The total weight of leaf produced by bilberry is known to be approximately equal to the weight of the current shoot. (Mork, 1946 a). In Fig. 46 the relationship between leaf weight and current shoot weight is shown for the material from Hamra and Garpenberg. The values for H/II and III were very close and have therefore not been distinguished; those for G/III (collected 1966) and G/IV (collected 1967) differed appreciably. It is not known whether the difference is between stands, between sites or between years; this problem is being given further study.

Figure 47 shows the relationship between leaf weight and total aerial shoot weight (including current shoots), for H/II and III. It

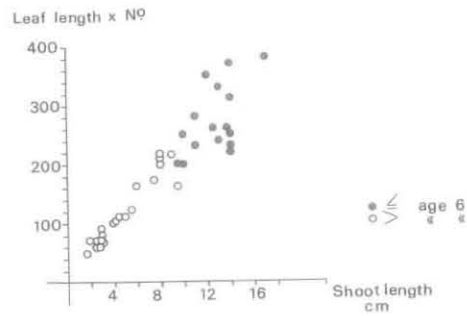


Figure 45. Length of leaf No. 4 times number of leaves, on shoot length, by two age groups.

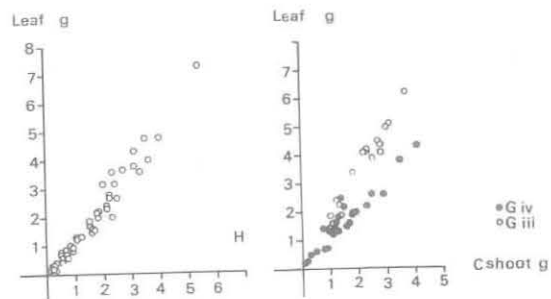


Figure 46. Relationship between leaf weight and current shoot weight for Hamra (left) and G/IV & III. Note divergence between the latter. (See text).

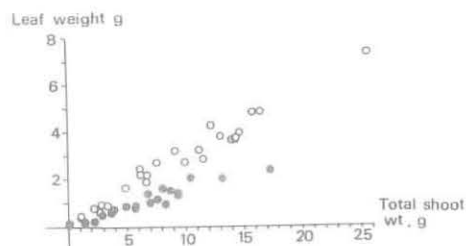


Figure 47. Relationship between leaf weight and total shoot weight, including C shoots, in H/II (filled circles) and H/III (open circles).

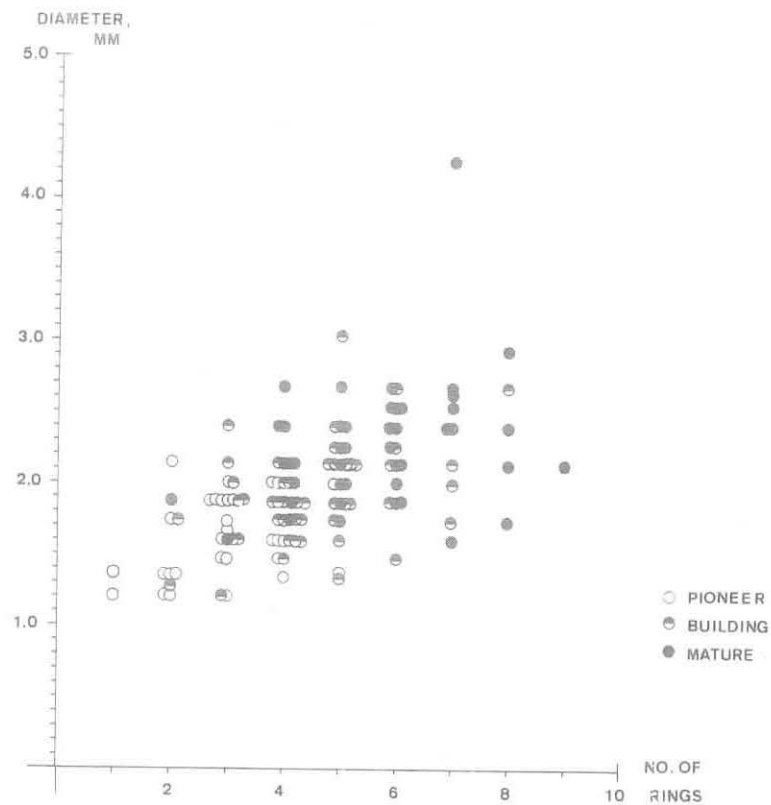


Figure 48. Diameter and age distribution of five largest stems at H/III, classified by the stage of the stand— pioneer, building and mature. Most of the younger stems amongst the five largest occur in the pioneer zone.

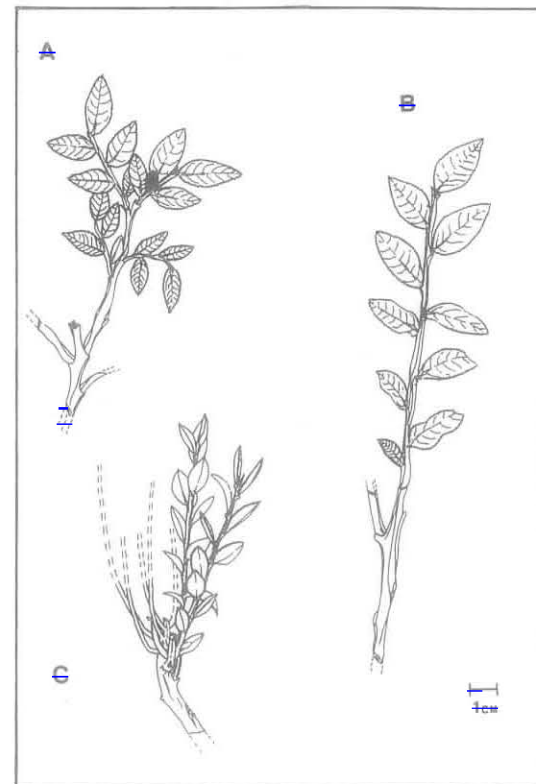


Figure 49. Environmental modification of growth. A, shade form of flowering shoot, B shade form of vegetative shoot, C shoots on same rhizome as B, but in exposed place. Compare leaf angle, size, etc.

is apparent that the stands differ in respect of the proportion of leaf to total shoot weight. There was no difference between G/III and IV, collected in different years; H/II and III were collected in the same year. Once again, this difference may be inherent or it may be environmental; clonal material from the two stands is now being studied to test this.

3.17 Environmental gradient ?

At H/III, it was possible, because of the sparse vegetation, to see clearly the stages in the development of the stand. The stand was classified into phases of development, pioneer, building and mature, where mature is equivalent to full cover. Figure 48 shows the distribution of the five largest stems between these three phases. The youngest, with the smallest diameter, were concentrated in the outermost zones, while the largest and oldest were in the interior. The building phase stems were intermediate in age and diameter.

This result is in accordance with centrifugal growth, but the differences may depend partly on environment. Stems of an age in the pioneer phase were of smaller diameter than those in the building and mature phases. This suggests that there were differences in the environment between the periphery and the centre. The zonation of mosses lends support to this; *Hylocomium splendens*, for instance, occurred only in the closed stand, *Dicranum* spp and lichens being dominant elsewhere. Zonation of this kind occurred in all the stands investigated and may represent a developmental sequence.

3.18 Plastic variation

Variation of shoot length with age, and consequently with position in the stand, has already been touched upon. Bright (1928) demonstrated that leaf size and current shoot length are influenced by the environment, the leaf being larger and the current shoot longer, in sheltered than in exposed places. Ritchie's similar observations on the effect of environment in clones of *V. intermedium* have already been referred to (Ritchie 1955b). Leaf size and angle also vary with light intensity and exposure, leaves being smaller in situations fully exposed to light than in those which are shaded, even on tillers on the same rhizome (see Fig. 49). Since differences in exposure interact with age differences, it would be of value to express the course of intrinsic variation for different environments, preferably for clonal material, so as to obtain a yardstick against which the plastic variation in different environments in nature might be compared. This leaves for the moment the problem of ecotypic differentiation untouched.

3.2 The short shoot

3.20 Introduction

The proportions of vegetative and flowering shoots vary with the age of the bush. According to Zlobin's classification of the phases of development, neither flowers nor fruit generally occur before the fourth year and do not become abundant until the fifth to eighth year (see Zlobin 1961 : stages III-IV, p.415). Flowering and fruiting remain abundant until about the thirteenth or fourteenth year but decrease thereafter. This may depend partly on site conditions, since older bushes at Cammachmore were still fruiting abundantly.

It is of interest to study the distribution of flowering shoots in relation to the age of the stand, and to estimate both the amount of fruit formed and the proportion that ripens. Since a part of the flowering shoots falls as litter, the distribution of these shoots is also of interest in this respect.

3.21 Distribution of short shoots and fruit

Figure 50 shows for H/II the relationship between the proportion of flowering shoots, the number of fruits at the time of sampling, the total length of the ten longest shoots, and the age of the oldest aerial shoot on each quadrat. The striking coincidence of these sequences is repeated in other stands studied. From their parallel development with the length of the ten longest shoots, it is concluded that they are similarly related to aerial shoot age, and to the tiller sequence.

The presence of fruit was not recorded continuously, and it is therefore likely that fruit production has been considerably underestimated. Table 12 shows average numbers of fruits, both for the 25 x 25 cm quadrats used in sampling, and after conversion, per m².

Stand	No. quadrats	Total fruits	Average/quadrat	No./m ²
H/II	23	78	3.39	ca 54
H/III	26	172	5.05	ca 81
G/IV	17	91	5.35	ca 86

Table 12. Average numbers of fruits at Hamra and Garpenberg, per quadrat and per m².

Since flowers are mainly solitary (about eight per cent of shoots in a sample had two flowers) each fruit is equivalent to a shoot. Some

of the short shoots as defined here are vegetative, some are sterile. Even after allowance is made for these shoots, a large difference remains between the number of fruits at sampling and the number of flowering shoots; this difference is substantially greater than that reported by Ritchie (1955a Tab.2). It is probable that most of the difference results from the loss of fruit between its formation and the time of sampling. Some fruit is formed after the second flowering period, but this is unlikely to have affected the present results.

Fruit production is reduced by numerous agencies, of which a few only need be mentioned here. Fungal infection and insect attack severely depress fruit formation and maturation. Insects damage the gynoecium by boring within a few days of the appearance of flowers. Fruit is therefore not formed. Fungal infection—possibly in association with insect damage—then reduces the number of fruits that mature. Some sites appeared to be more affected than others by such damage. About 35 per cent of a sample of flowers from Skogshögskolan was damaged by insects, and of 91 fruits collected from G/IV in 1967, all but one were unripe, "mummified" or damaged by insects. In contrast, all fruits collected at Hamra in that year were superficially sound. (Cf. Perttula 1941, p. 115).

Frost damage is another factor which is important, not only as a reducer of fruiting, but also as a potent agency in killing entire shoot systems (cf. Havas 1965). Shoots exposed above the snow, particularly during the late winter when insolation may be intense, are frequently killed back. The flowering shoots, on the upper part of the axis, are especially liable to this. Not only does this reduce flowering (perhaps for several years, since it may cause a new phase of vegetative growth), it also increases the litter fall.

3.22 Distribution of litter fall

Figure 50 shows the distribution of flowering shoots, long shoots and fruit in H/II. It should be recalled that there is a relationship between total shoot length and the length of the longest shoots; leaf weight is, as might be expected, also greatest at the points at which the length of the long shoots is greatest. Litter is made up of four major components:

- 1) Leaf,
- 2) Shoot, subdivided into (2.1) shoots from withered axes,
(2.2) current short shoots,
(2.3) current long shoots
- 3) Fruit,
- 4) Flower remains, etc.

Thus the total litter fall from a bilberry stand each year consists of the year's leaf production (less that removed by insects and herbivores) plus most of the fruit and floral parts; in addition, a proportion of the long and short shoots (subject to losses by consumption). Examination

of tillers throughout the course of their development indicates that although long shoots are lost as litter in the year of their formation, the major losses of such shoots occur when an entire axis withers. Breakdown occurs over a period of years; attempts have been made to estimate for how long dead stems remain standing, and suggest that three years is the maximum. This may vary from one site type to another. Further investigations are in progress. The loss of short shoots occurs more generally and must contribute appreciably to the litter, but no reliable estimate can be made. However, the distribution of the litter fall throughout the stand may be seen from Fig. 50; most fruit, flower and leaf litter will fall in the parts of the stand where the long shoots reach their greatest length, i.e. in the region of overlap between tiller systems, hence probably among the middle-aged and older bushes, cf. Cormack & Gimingham (1964).

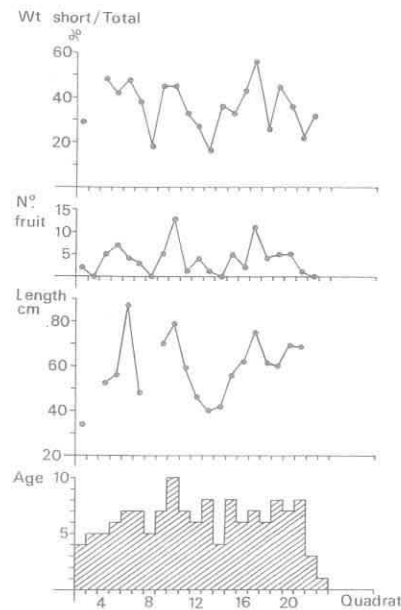


Figure 50. Relationship between percentage of flowering shoots, fruiting and the length of the longest shoots, with the age of the oldest bush for reference. Total shoot length is also greatest at these points, and leaf weight; hence litter fall should be at a maximum in these parts of the stand.

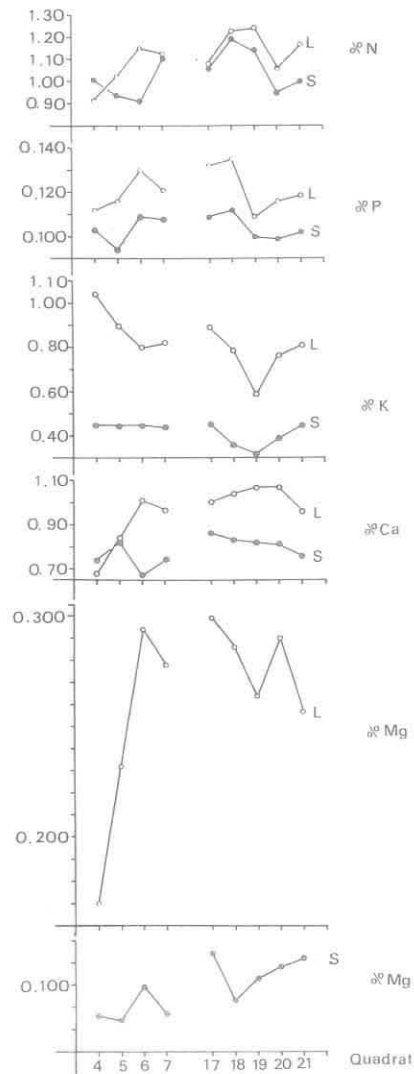


Figure 51.

Mineral nutrient contents in leaf and shoot of a subsample from H/II, in relation to position in the stand. Only quadrats at opposite ends of the transect were analysed. Spatial variation in Mg content of leaf (L) was particularly striking, 1967.

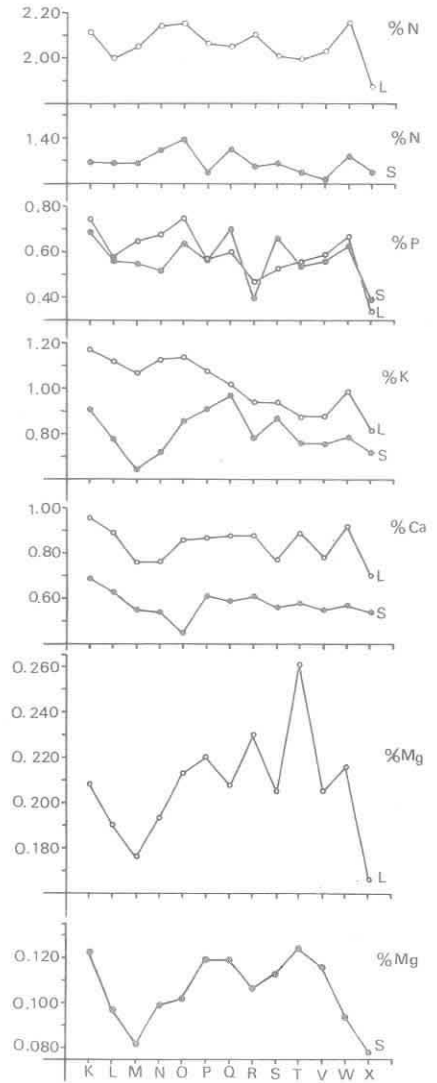


Figure 52.

Mineral nutrient contents in leaf and shoot of a subsample of quadrats in G/IV. Cf. average values in H/II, 1967.

4 Mineral nutrients in the aerial shoots

4.0 Introduction

In view of the relationship shown to exist between the age structure of the stand and other characteristics, it was thought to be of interest to discover whether the mineral nutrients also varied with age and position in the stand. Possible differences in the mineral nutrient content of the stands at Hamra and Garpenberg were also of interest.

Trevett (1959, Fig. 7, 8, 9) showed for *Vaccinium angustifolium* and its hybrids in Maine the course of seasonal variation in N, P and K content of leaves and shoots. This is relevant in the present case, since there is reason to believe that the course of variation will be similar in bilberry. Mork (1946, Tab. 7, 11), who also published analysis values for various plant organs in bilberry (samples from a fjeld forest and a lowland forest), made the point that mass analysis of the plant (and indeed, of other dwarf shrubs) is undesirable, because of the influence of the proportion of older stems on the results. Both he and Trevett emphasised that the time of sampling is important—Trevett also suggested that sampling "...should coincide with the period in which specific plant developments are occurring."

In a later paper, Trevett and his co-workers (Trevett et al. 1968) published data concerning the seasonal trend of many nutrient elements in the leaves of clones of *V. angustifolium*. Several periods of fairly constant composition were observed, some related to clearly distinguishable growth phases, e.g. terminal dieback. It was considered that the phase of terminal dieback was a critical period for the formation of fruit buds, an important consideration in the case in point. One important difference between the "blueberry fields" on which the above studies were made, and natural stands of bilberry, is age. The commercial fields are regularly burned to promote the growth of new shoots; hence analyses are made on shoots which differ essentially in respect of the length of time which has elapsed since the latest burn. This is usually a matter of weeks. In the uneven-aged stands of bilberry, the age range is far greater; hence C shoots and leaves collected for analysis are derived from a population of the variability of which may be so great that critical comparison of differences may not be possible.

It is conceivable, however, that the regularity of age structure in bilberry stands may cause average values from different stands to be comparable, i.e. since they are drawn from comparable structures. There are two major objections to this; in the first place, the average age of tiller populations differs quite considerably (cf. Fig. 26). If mineral nutrient composition varies with age, then comparison of values from stands of different ages is subject to error of unknown extent. In the second place, mineral nutrient analysis is a technique intended for precise application. If the material to which it is applied is incapable of comparison ab origo, nothing is to be gained by analysing it. The levels and differences which it is desired to determine

Quadrat	Material	%N	%P	%K	%Ca	%Mg
3/H/III-1	C long shoot	0.87 0.87	0.107	0.32	0.34	0.051
	C flowering shoots	1.11 1.12	0.118	0.32	0.49	0.058
	Leaf (joint)	0.90 0.89	0.120	0.82	0.60	0.179
9/H/III-1	C long shoot	1.10 1.08	0.120	0.38	0.47	0.091
	C flowering shoot	1.16 1.21	0.126	0.42	0.57	0.087
	Leaf (joint)	1.09 1.08	0.133	0.85	0.77	0.184
11/H/III-1	C long shoot	1.06 1.09	0.121	0.40	0.47	0.105
	C flowering shoot	1.32 1.32	0.138	0.41	0.61	0.100
	Leaf (joint)	1.12 1.10	0.140	0.81	0.88	0.225
15/H/III-1	C long shoot	1.17 1.17	0.132	0.42	0.51	0.103
	C flowering shoot	1.42 1.43	0.142	0.42	0.65	0.094
	Leaf (joint)	1.22 1.18	0.171	0.77	0.91	0.225

Table 13. Distribution of mineral nutrient elements in various plant organs, and variation in mineral nutrient content with location in the stand, H/III, September 1967.

will be obscured by the intrinsic variation.

Studies from other fields make it clear, that whether or not the mineral nutrient content varies with age, variation occurs from one year to another. It is therefore necessary to sample over several growing seasons. The present investigation is deficient in respect both of this requirement and of the requirement outlined by Trevett. It is nevertheless possible to study the mineral nutrient content of C leaves and shoots in relation to the position of the sample in the age sequence. This may give indications for future work on a sounder basis.

4.1 Variation with position in the stand

Table 13 shows the variation in mineral nutrient content with position for four quadrats in H/III-1. For the current vegetative shoots, the content of all mineral nutrient elements studied increased from the periphery to the interior of the stand. For current short shoots (as defined here) N, P and Ca increased clearly, while K and Mg tended to increase. For the leaf (joint samples from long and short shoots) N, P, Ca and Mg increased, but no definite increase occurred in K. The N, P and Ca content of the short shoots was consistently higher than that of the vegetative shoots.

Figure 51 shows the mineral nutrient content of current long and short shoots and leaves from H/II (collected Sept. 1967). Material from quadrats at both ends of the transect was analysed, to test for possible effects of quadrat position and symmetry. Leaf N, P, Ca and Mg increased into the stand in quadrats 4-7, the increase being marked in Mg. Leaf Ca and Mg increased into the stand in quadrats 21-17. Shoot N, P and Ca showed no consistent increase at either end of the transect. Variation was large within the closed stand for leaf N, P, K and Mg, but less so in the shoots. Leaf contents of all elements were generally higher than shoot contents, but this situation was reversed on two quadrats. No consistent relationship was observed between leaf and shoot contents.

Figure 52 gives the same information for quadrats K-X of G/IV (collected July 1967; in view of differences in latitude, altitude and exposure, the times of collection of H/II and G/IV were probably equivalent as regards development). All mineral nutrients increased distinctly from marginal quadrat X to quadrat W. The edge of G/IV was more clearly defined than that of e.g. H/III, and the transition to the closed stand was almost immediate. Leaf contents of N and P seemed less variable than in H/II, but strict comparison is difficult. Except in the case of P, leaf nutrient contents were consistently higher than shoot contents and variation in the two was generally more closely parallel than that in H/II.

Differences between mineral nutrient content in the peripheral and inner parts of the stand thus appear in three stands. However, variation was so large and the number of samples so small in relation to it, that this trend cannot be satisfactorily established. No consistent relationship is evident between leaf or shoot mineral nutrient contents and any character demonstrably associated with age. Nevertheless, in G/IV, otherwise a relatively uniform stand in respect of most of the other characters studied, there were large variations in mineral nutrient content. It still remains to discover their cause. It may be that they are random, but it seems more probable that they are related to some difference within the plant. In view of the reservations expressed above regarding the analysis of material from an uneven-aged population, future work should concentrate upon individuals of known age, to test whether age and nutrient content are related. In view of the spatial variation in mineral nutrient content in forest soils (Troedsson & Tamm 1969), it will be difficult to establish causal relationships between plant nutrient levels and the soil contents of the nutrients in question. The problem might, however, be approached experimentally, using clonal material.

4.2 Variation between stands

The limitations of the material make its use for comparison of mineral nutrient content at Hamra and Garpenberg of doubtful value. A gross indication of the relative position of the stands may be obtained. Table 14 shows average leaf and shoot contents for G/IV and H/II, collected in 1967. The variation in the material (particularly in Mg and K) makes the average values for these elements uncertainly representative. Leaf values for G/IV were higher in N, P and K than those for H/II but lower in Ca and Mg. Shoot values for G/IV were higher in N, P and K and similar in Mg, but lower in Ca, than those from H/II. The coefficients of variation were almost invariably too great for strict comparison to be possible.

Leaf	G/IV	H/II	Shoot	G/IV	H/II
N %	2.06	1.11	N %	1.30	1.03
P	0.159	0.121	P	0.157	0.104
K	1.01	0.82	K	0.81	0.41
Ca	0.84	0.96	Ca	0.57	0.78
Mg	0.207	0.264	Mg	0.106	0.098

Table 14. Average content of mineral nutrients in leaf and shoot of G/IV and H/II in 1967, per cent.

Values for shoots of H/III (1967) resembled those for H/II as regards N, K and Mg, but were higher in P and lower in Ca. Shoot

of G/IV (1966) had values of N, P and Mg resembling the 1967 values, but K was lower and Ca higher. The leaves were frosted during collection and were therefore not analysed.

On the basis of this small material, it can only be concluded tentatively that the leaves of G/IV contained more N, P and K, about as much Ca and less Mg, than those of H/II in 1967. The shoots of G/IV in 1967 contained more N, P and K, less Ca and about as much Mg, as those of H/II. These differences in N, P and K probably reflect differences between the sites in respect of these elements, but environmental differences, e.g. in light and water, may also have played a part. Further investigation of this problem is desirable.

5 Summary comparison

5.0 Introduction

An aim of this investigation was to discover whether age could be used as a common factor in comparing bilberry populations. It has been shown that much of the variation in a stand can be ascribed to age differences. In this section a summary comparison is made of the stands studied, mainly those at Hamra and Garpenberg.

5.1 Standing crop and yield

5.11 Leaf

Table 15 summarises information concerning leaf weight by stands and years. Leaf weight differed greatly between stands, even in the same year and on the same site. Variation in leaf weight at sampling was especially great between quadrats, presumably as a result of the way in which the transect cut across the age sequence of tillers.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Quadrats	25		17	23	28
Average	1.676		3.563	0.922	2.463
g					
Median	1.520		4.075	0.939	2.552
Range	4.080		4.705	2.284	7.216
s^2	0.779		1.797	0.434	3.036
CV %	52.69	(1)	37.41	71.51	70.76

Table 15. Data on leaf weight by stands and years. Note (1) Leaf of G/IV frosted during collection, weights subject to error. Note that the number of quadrats differs slightly in the following tables, owing to the exclusion of those which had incomplete information.

5.12 Current shoot

Table 16 gives similar information for current shoot weight. Here comparability is rather more complete than is the case with the leaf. The weight of current shoot at G/IV in 1966 was very similar to that in 1967, but G/III (1966) was only about 70 per cent of that at G/IV (1966) and was more variable. Hamra II and III also differed greatly, H/II having only half the weight of H/III. Both were about equally variable and slightly more so than G/III.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Quadrats	25	8	17	22	27
Average g	1.498	2.116	2.117	0.921	2.014
Median	1.361	2.199	2.255	0.806	2.080
Range	3.979	2.871	2.647	2.255	5.264
s ²	0.918	0.687	0.651	0.395	1.679
CV %	63.96	39.19	38.12	68.28	64.34

Table 16. Data for total current shoot weight by stands and years.

Table 17 shows total production (leaf + current shoot) for the stands, including G/IV, for which leaf weight is slightly lower than it should be (see note, Tab. 15). Total production is of course the sum of the weights and therefore varies in the same way.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Yield	3.174	5.66 ¹⁾	5.680	1.843	4.477

Table 17. Total production of leaf and current shoot by stands and years. Note 1) : leaf weight slightly underestimated, total therefore approximate.

5.13 Shoot length

Table 18 shows both the average length of individual current long shoots and the average total length of all long shoots on the quadrat, excluding G/IV, where only the ten longest shoots were measured. The difference in average individual shoot length between H/II and III is relatively small, but that in total shoot length on a quadrat is very large. Garpenberg III resembled H/III rather closely in respect both of average shoot length and total shoot length, and was similarly variable in respect of the latter. (See also Tab. 10; the slight differences depend on rounding discrepancies).

Stand	G/III	H/II	H/III
Quadrats	25	19	23
Individual length, mm	44.7	43.6	49.6
Total length, mm	2984	1182	2852
s ²	55.49	114.53	56.58
CV %	16.66	24.54	15.16

Table 18. Individual current shoot length and total shoot length on a quadrat.

5.14 Standing crop

Table 19 shows the average aerial standing crop, i.e. leaf, current shoot and older shoots (but excluding fruit, of negligible dry weight). Standing crop represents the accretion of plant material by growth over a period of years, less litter and consumption. It may be regarded as the net statement of the growth of the stand, and more direct comparison should be possible than is the case with production. Garpenberg IV (1967) had clearly the largest standing crop, almost twice that of G/III, which was most closely comparable with it in respect of the age of the tillers, although having a smaller area. It was also least variable. Garpenberg IV (1966) was intermediate between them (see note in table). Hamra II had the smallest standing crop, less than one-third that of G/IV (1967) and about half that of G/III. Hamra III was between H/II and G/IV (1966) in respect of standing crop, but was most variable of all.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Quadrats	25	8	17	23	28
Standing crop, g	13.94	17.65	24.46	7.02	10.88
Median	13.42	(1)	24.86	6.65	9.66
s ²	63.60		69.57	23.73	62.25
Range	27.98		28.51	19.57	32.66
CV %	57.22		34.14	69.40	72.51

Table 19. Total standing crop on a quadrat. Note (1) : data for G/IV underestimated as regards leaf weight. Included only for purposes of comparison.

Table 20 shows the weight of aerial shoot without leaf, i.e. minus leaf litter but including a proportion of current shoots and older shoots which will fall as litter. The relative position of the stands is unchanged and variability is little affected.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Quadrats	25	8	17	23	28
Weight, g	12.25	14.13	20.92	6.09	8.41
Median	12.16	14.83	21.20	5.80	7.22
s ²	50.97	31.63	51.00	17.97	38.45
Range	25.44	20.88	24.00	17.28	25.46
CV %	58.22	39.80	34.13	69.54	73.74

Table 20. Average aerial shoot weight (standing crop - leaf).

5.15 Rhizome weight

Total rhizome weight is the net result of many years' accretion, but unlike aerial shoot weight or standing crop, is less subject to casual losses, although it is apparent that consumption losses occur. Hamra II had the least rhizome weight, about half that of H/III, which was slightly more variable. Garpenberg IV (1967) had the greatest rhizome weight and was least variable. Garpenberg IV (1966) had considerably less rhizome but was similarly variable—the increase in rhizome weight in G/IV seemed to be progressive across the stand. The rhizome weight of G/III was similar to that of G/IV (1966) and was most variable of all. See Tab. 21 below.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Quadrats	28	8	17	23	28
Weight, g	17.61	18.14	28.63	11.01	21.51
Median	17.22	15.30	28.51	12.37	20.59
s ²	168.33	35.11	91.81	48.01	219.12
Range	61.11	14.96	37.04	24.49	53.69
CV %	73.42	32.67	33.46	62.92	68.80

Table 21. Total rhizome weight.

From the information in tables 20 and 21, the total biomass for each stand may be obtained, or in strict terms, accretionary biomass (total biomass - leaf; but this excludes current shoot losses). The different years of collection of the G/IV material make it desirable to treat the two quadrat series separately. Garpenberg IV (1967)

had clearly the greatest biomass (49.55 g), followed by G/IV (1966) (32.27 g). Considered as a whole, G/IV still had the greatest biomass, viz. 40.91 g. There was no real difference between G/III and H/III, although the latter was very slightly the greater (29.86 g, 29.92 g). Hamra II had the least biomass (17.10 g). Age differences between the stands are not taken into account here; it is, however, probable that an old stand would have a greater biomass than a relatively young one, largely as a result of the more intensive exploitation of the site. This is also a point to consider when making comparisons between stands in terms of crude biomass.

5.2 Mineral nutrients

This aspect of the stands is discussed in section 4, and information is summarised in Tab. 13 and 14.

5.3 Growth-integrating characters

5.31 Basal area

Table 22 shows the average basal area of the five largest stems on each quadrat, including Cammachmore I and II, united here.

Stand	G/III	G/IV	G/IV	H/II	H/III	Cm
Year	1966	1966	1967	1967	1967	1969
Quadrats	25	8	17	23	26	2
BA ₅ , mm ²	26.8	35.4	45.1	14.3	15.6	130.5
Median	27.9	37.9	44.5	16.6	15.1	-
s ²	157.44	95.89	35.00	44.84	35.45	-
Range	46.5	28.9	20.9	25.0	27.3	-
CV %	46.82	27.66	13.11	46.82	38.16	-

Table 22. Basal area of the five largest stems on each quadrat, including Cm I and II.

Hamra II and III had closely similar basal areas, but H/II was the more variable. Garpenberg IV (1966) had a lower basal area than did G/IV (1967), which was least variable of all. Figure 8 shows that there was a marked trend across G/IV in both aboveground and underground weights. The different years of sampling should in theory play no part in this difference. The basal area of G/III was distinct from that of the Hamra stands and resembled G/IV (1966), although it was considerably more variable. It differed as much from G/IV (1967) as from H/II and III.

The two Cammachmore quadrats were united here, since they seem to be representative of the stand. Their average BA_5 was about three times that of G/IV (1967) and about nine times that of the Hamra stands. No figures are yet available for standing crop, but ocular estimates suggest that this is commensurate with the difference in basal area. Even when allowance is made for age differences, the gap is still as wide.

5.32 Diameter

Diameter growth has already been discussed in section 3, including the differences between tillers of the same age. It is clear from the scatter diagrams that there were differences between stands on the same site. This raises the question of whether the apparent differences in diameter represent, in the first place real differences, and in the second place, differences between the sites which the averages refer to. Diameter, however, is only one dimension of growth; basal area differences are more appropriate biologically. Figure 53 shows the average diameters of Fig. 18 converted to terms of basal area. When it is considered that standing crop appears to increase linearly on basal area (at least, as regards BA_5 within the range of the material), it is apparent that the weight of a tiller with a basal area of ca 7.2 mm^2 will be appreciably greater than that of another with a basal area of ca 4.6 mm^2 , at the same age. This, for instance, represents the difference in basal area between eight-year-old tillers at Garpenberg and Hamra.

Thus while comparison of diameter growth gives an impression of differences between stands, it does not point sufficiently clearly to the effective differences in overall growth. The use of basal area, however, accentuates these differences, while retaining the advantage of being comparable over the age range. It is desirable to be able to express growth in terms of total basal area, i.e. on a population rather than an individual basis; Tab. 6 indicates the beginning that has been made on this.

5.4 Ranking

The summary comparison made here of characters used for expressing growth in the stands studied suggests that the accretionary characters were most suitable for ranking the stands, as compared with "production" characters, i.e. yield of current shoot and leaf. The latter are inevitably affected by accidents such as grazing, which may result in an underestimate of weight. They also vary from year to year and therefore require to be sampled over several growing seasons. If the object of an investigation requires only that yield be known, so that it can be related to e.g. consumption, there is no limitation on its use. If, on the other hand, it is necessary to study and compare net accumulation of plant material in relation to yield, then age must be introduced. Those

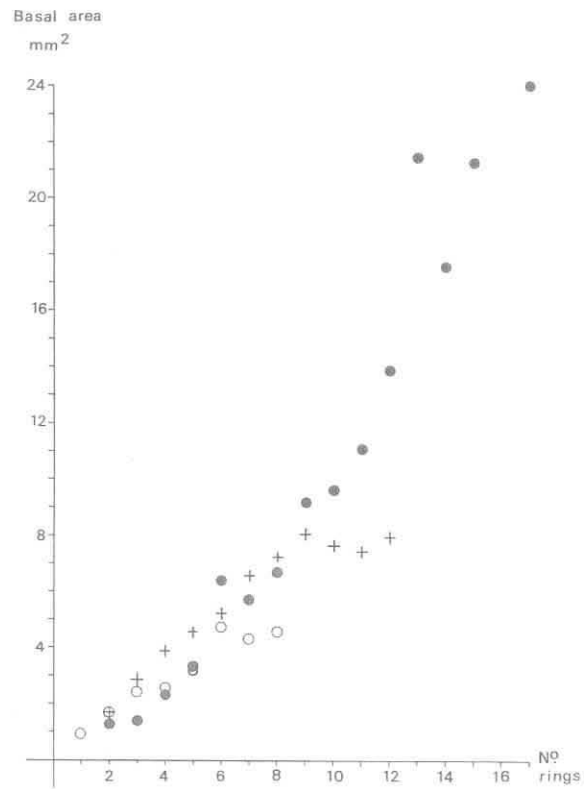


Figure 53. Mean values for basal area on age for the Hamra, Garpenberg and Cammachmore populations. Cf. Fig. 18, and note that the relatively small diameter difference at any age is accentuated by being expressed in terms of basal area.

accretionary characters, such as standing crop or biomass, when compared, should be compared at the same point in the growth cycle; this point will be taken up in the Discussion. Diameter or basal area increment are directly comparable because of their being expressed in relation to age. They have the advantage that they are a fossil record, not subject, for the individual tiller, to casual losses as are yield characters.

The stands studied here may be ranked according to any of the characters reviewed in this section. Table 23 summarises their relative position in respect of the various characters.

Stand	G/III	G/IV	G/IV	H/II	H/III
Year	1966	1966	1967	1967	1967
Leaf wt	3	-	1	4	2
C shoot wt	3	1	1	4	2
Yield	4	2	1	5	3
SC	3	2	1	5	4
Aerial shoot	3	2	1	5	4
Rhizome wt	4	3	1	5	2
BA ₅	3	2	1	5	4
Biomass	3	2	1	4	3

Table 23. Relative rank of stands in respect of various characters.

One of the chief problems here is that of separating stand or site differences from differences between years of sampling. The relative rank of the stands is clear only as regards the extremes; there is no doubt that G/IV was in general first in rank, and H/II last. In a study where sampling was undertaken over a period of years, it might be possible to remove the difference in year of sampling. This applies particularly to yield. Thus H/III had a higher yield of leaf and current shoot than G/III, but in different years. Where accretionary characters are concerned, H/III had a higher rhizome weight than both G/III and G/IV (1966), and was ranked with G/III in respect of biomass.

If the stands on each site are combined, on the assumption that they are representative for the site as a whole, then in all characters the Garpenberg site is ranked before the Hamra site — notwithstanding the very marked differences within the two sites. Even when the yield characters are excepted from the comparison, the differences remain.

Discussion

Circular and arcuate patches are not uncommon amongst plants with rhizomes or prostrate stems. The arcuate form develops from the circular by decay of the centre and continued centrifugal growth. Centrifugal growth is a consequence primarily of rhizomatous or prostrate habit, but depends for its full development on relative uniformity of environment. Ideally the product of such expansion would be a generally circular individual having its youngest shoots at the perimeter and its oldest at the centre. Death of the oldest parts would leave a ring-shaped individual. Eccentric growth may result from the dominance of one axis of the plant or, as is the case in exposed places, from the influence of the prevailing wind.

Examples are plentiful. Arctostaphylos uva-ursi is a case in point. In this species the process has been described as follows: "An freien Plätzen aber breitet sich Arctostaphylos allseitig aus, ... Die zentralen Teile eines Individuums sterben allmählich ab und die Wanderung der natürlichen Ableger setzt sich zentrifugal fort. ..." (Grevillius & Kirchner 1923; though there are contradictory statements to the effect that the plant dies with the death of the primary root).

At this point, definition of the "individual" becomes difficult. Each stem axis of the original plant when severed from it and in possession of adventitious roots, is a new individual but genotypically identical with the other axes of the plant. Decay of the severed main axis may proceed until lateral branches themselves are released. During this time the centrifugal growth of the distal shoots continues; the plant assumes the form of a ring, other species perhaps occupying its old centre. Such rings may expand until their relationship is no longer apparent. Another case is that of Pteridium aquilinum. Oinonen, building partly on the earlier work of Watt, has demonstrated for Pteridium that individuals, in the form of vastly expanded arcs and circles, may persist for very long periods and that fragmented clones derived from them can be recognised (Oinonen 1967, Watt 1947a).

In bilberry, sympodial growth results in a highly branched system having acute angles between the branches — as may be seen in the aerial shoots. Such a system, when confined to one plane, as is essentially the case in the humus, fans out, and adjoining fans overlap. The rhizome branches that arise from the primary rhizome after some years go through the same process, but the lag in time is expressed as a gap in space. The result of this is a series of "waves" of young rhizome at intervals which represent a period of about three years.

Continued centrifugal growth of the type outlined for Arctostaphylos results in a hollow stand, whereas in the case of Pteridium, a mosaic of phases remains behind the advancing front (Watt 1947a). The

situation in bilberry seems to be analogous to that in Pteridium rather than to that in Arctostaphylos. Zlobin's observations indicate that a stand gradually becomes senescent and that degeneration spreads from the centre (Zlobin 1961 : Fig. 2-5), gradually encompassing the entire stand. It is, however, somewhat difficult to conceive of an entire stand's becoming degenerate, in view of the release of propagules by decay and insect larval attack. It seems more likely that a situation similar to that in the hinterland of Pteridium should arise.

The factors controlling the rate of rhizome decay remain obscure. Little appears to be known about the extent to which rhizome systems can remain physiologically active in their older parts when assimilating organs are confined to the distal part of the system. Kershaw (1964) suggested, with reference mainly to Alchemilla alpina, that the balance between respiration and photosynthesis was decisive. An extensive, and presumably actively respiring, rhizome system might weight the balance heavily on the negative side under certain circumstances. Any propagules released by the advance of decay from the older end of the rhizome might, as is perhaps the case in Alchemilla, be ideally situated to continue active growth; release would almost immediately provide "...an excess of metabolites relative to the now small rhizome system ..." (Kershaw 1964). It should be emphasised that no observations on the physiology of bilberry rhizomes appear to be available—the lack of them is not confined solely to bilberry—for which reason the above explanation must remain speculative.

The above interpretation of the structure of the bilberry stand implies that it is clonal, which accords with the general habit of related species of Vaccinium. It is also the simplest explanation of the spatial relationships encountered. Nevertheless, it does not imply that all stands of bilberry are homogeneous or that they exhibit all the features described here. The structure must, however, be fundamental to the biology of the plant, and accords with other workers' conclusions.

Each rhizome unit may be regarded as representing a sequence in time, a productivity curve of an upgrade-downgrade process (cf. Watt 1947). The curve has two components—rhizome and tillers—the individual curves for which are superimposed, but out of phase. The rhizome curve may be used as the basis for the time scale. The pioneer rhizome spreads out ahead of the tiller stand and the old rhizome extends behind the living tillers which arise from it. For the overlapping rhizome units that form the stand, the maximum of accumulation (on an areal basis) seems to be at an age of 12-14 years (using the Garpenberg material as base). At this age, total biomass is at a maximum. Rhizome weight reaches equilibrium—when growth and decay are in balance—at an age of about 20 years, and the quadrat population at

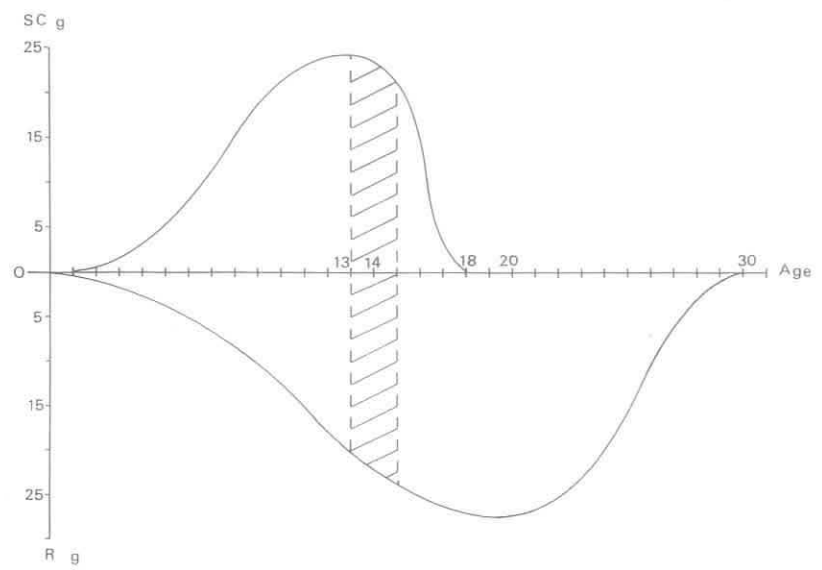


Figure 54. Empirical productivity curve for the rhizome unit, based on Garpenberg material. Age is expressed in terms of the rhizome. Points of significance only indicated. Note period of maximum biomass (hatched).

age ca 12 years. The greatest biomass is attained at rhizome age ca 14 years. Thereafter, rhizome weight continues to increase, while shoot weight decreases. Assuming that the oldest bush on the rhizome has become litter by the age of about 17 years, after having stood moribund for two or three years, the aerial shoot curve will decline to zero at rhizome age 18 years. The rhizome curve reaches equilibrium at age ca 20 years and falls to zero by age 30 years, when all the old rhizome of one generation has decayed. Figure 54 represents this course of development.

Centrifugal growth implies that the zone of maximum accumulation will move outwards, one such zone following the other. Marginal effects, such as those described by e.g. Watt (1947), Kershaw (1962), Ovington (1953), may occur; this may be the explanation of the marked double peak in G/III. However, the interior of G/IV suggests that equally pronounced peaks may occur within the outermost peaks, for which reason the above explanation may not be the only one. If degeneration begins in the interior of the stand, it is to be expected that this will be reflected, perhaps less in the rhizome, than in the aerial shoots. The apparently vigorous growth of tillers in the middle of the stand, and the high standing crop, argue against this, at least as regards the stands studied here.

The structure of the tiller population is basically determined by rhizome morphology; thus the disposition and sequence of the senior tillers depends primarily on the rhizome. Secondary branches of the rhizome, which arise after several years, eventually give rise both to orthotropic terminal shoots and to tillers from lateral buds. These grow up into the stand which is already established—a process that might be termed "filling in"—as was the case in H/III. The number of tillers per unit area increases as a result of this, forming the closed stand. This situation might be considered to parallel that in stands of Pteridium (Watt 1947 : Tab. 4).

In forest stands, the total basal area increases as the number of stems increases, up to a point; this represents the carrying capacity for that species on that site under the circumstances obtaining. Stands on the same site, having the same total basal area but different stand density, have different average stem diameters. It is supposed that an analogous situation exists in bilberry (cf. Tab. 6) as regards the quadrat tiller populations. An important difference, however, is that in the bilberry stand the population is a clonal hierarchy.

Each year, a number of tillers grows into the population. The origin of these tillers is of interest. Not all arise from terminal buds, but the rhizome apices which grow into an area each year may be an important source of recruitment into the stand. The process whereby orthotropic shoots originate has been described by Barker & Collins (1963), who cultured V. angustifolium rhizome in vitro. They found the rhizome to be "...extremely light sensitive..." and it "when struck by light, even light at the safe ... plant wavelength and at a low intensity, will respond by adopting an ageotropic posture and by terminating shoot extension." The sensitivity to light appeared to be seasonal, maximum sensitivity occurring in late summer. Similar sensitivity certainly ex-

ists in *V. myrtilus*, although nothing appears to be known about seasonal effects. If rhizome tips in the upper part of the humus or in the litter layer are light-sensitive, they will undergo reorganisation and will form orthotropic shoots. Rhizome apices are abundant in these strata, but it is an open question whether light intensity under the closed stand e.g. at Cammachmore, is adequate to initiate reorganisation. In the less dense Swedish stands studied, light intensity is far higher. If sensitivity extends into the leafless period, tiller initiation might also occur in the denser stands.

Tiller initiation is one matter; ingrowth and survival are another. The concentration of dead tillers in the youngest age class at Cammachmore suggests that competition may be intense at this stage. Since no information could be obtained about orthotropic shoots which failed to become established after initiation, it is difficult to estimate the total mortality at this stage. Attempts were made to assess annual ingrowth by applying a correction based on the assumption of a constant mortality rate, to the tillers in each age class. Examination of this assumption showed that it was not strictly correct, although the deviation of the survival curve from the diagonal straight line representing constant mortality was not great, i.e. it could not be said to approach the highly convex curve characteristic of populations which live out their inherited lifespan, all individuals dying within a short time of one another (Odum 1959).

If in the Cammachmore stand maximum carrying capacity has been reached, the survival of ingrowing tillers may be determined largely by the opportunities made available by the death of a senior tiller. The calculated mortality rate for this stand (on the above assumption) was 0.57, that is, approximately four tillers in seven years. The five largest stems had an average basal area of ca 26 mm² in a total basal area of ca 600 mm². The death of one senior tiller would release at least 26 mm², with its associated demands on space and resources. Part of this would immediately be taken up by other tillers, but some might become available for ingrowing tillers. This explanation depends on the assumption of full occupation of the site, which in view of the smallness of the sample, may be unjustifiable. Nevertheless, it is an assumption that could be tested, not only by further sampling, but also by experimental means, analogous to a thinning.

It is disputable whether populations sampled in this way can legitimately be subjected to population analyses of the type used by e.g. Harper (1967). It is, however, considered that an age analysis carried out on harvested material fulfils the requirements for population analysis. The age distribution of individuals, and hence their longevity, is probably obtained as effectively by the harvesting method as by longer-term population studies. The disadvantages are that ingrowth and mortality rate cannot be directly measured. The rate of breakdown of standing dead stems cannot be determined. These disadvantages might be overcome by combining the two approaches. Experimental modification of stands, carried out at the same time, would give valuable additional information.

The stands in respect of BA_5 , BA_{tot} and in the course of a increment in individual tillers. These differences were associated with differences in standing crop, biomass and ultimately, in the weight increment of individuals. If in general terms basal area at a given age reflects the growth performance of a species on a site, then the differences found here should reflect a difference in the quality of the sites in respect of the growth of bilberry. Does this difference bear any relation to the quality of the site for growth as such ?

Although the course of increment may be comparable, it does not follow that the stands themselves are comparable. For instance, the range of site types may bear a range of ecotypes, or the extremes may be ecotypically differentiated. The individual clones studied here may differ so greatly that they are not representative of the site. Disregarding for the moment the numerous forms described (listed e.g. by Hegi 1927), the occurrence of which bears apparently no relationship to site differences, there is no unequivocal evidence in the literature that the morphological differences found over the range of sites occupied by bilberry are inherent rather than plastic (Ritchie 1956; but cf. also Havas 1965). This may, however, be merely a consequence of the lack of information on this point. Differences between clones, e.g. in respect of morphology and pigmentation, serve to distinguish them in the field, and are well known amongst N. American species of *Vaccinium*. The basis of these differences, and the existence of ecotypes, must, however, be established by experiment. But it is not enough to demonstrate that inherent differences exist; it is necessary also to show that the differences are directional and that inter-clonal differences on the same site are large enough to obscure differences between sites. Since it is likely that variation over the range of sites is continuous, rather than discrete, large inter-clonal differences would make comparison of sites difficult.

The concept that the field layer vegetation expresses the constellation of environmental factors which make up the forest site type is a sine qua non of this system of site classification. It is the basic principle of Cajander's system and of the systems analogous to it, and is, for instance, expressly stated by Arnborg (1953). If in the range of species represented over the spectrum of forest site types, no ecotypic differentiation exists, then the growth of these species — by extension, of any one of them — should reflect the environmental differences between the sites. However, for at least one important component of the vegetation, *Calluna vulgaris*, ecotypes have elsewhere been shown to exist.

It remains to be seen whether individual species can be used as a means of studying the growth environment on forest site types, and to discover in what way and to what extent their growth is related to the environment and to that of the other components of the community.

The specific objects of this study were first, to discover the relationship of the aboveground to the underground parts of the plant; secondly, to discover how standing crop, production and performance vary

throughout the stand; thirdly, to discover whether age could be used as a common factor in comparisons, and fourthly, to discover whether stands could be more satisfactorily compared in terms of growth rate than in terms of standing crop and production.

As regards the first object, the dynamic relationship of the rhizome and aerial shoots has been demonstrated. The relationship of stand characters to the age sequence has been demonstrated, although in certain cases the interaction with environment could not be separated from the intrinsic differences. As regards the use of age as a common factor in the comparison of stands, it is suggested that accretionary characters, principally biomass of stands, may most suitably be compared at the point in the growth cycle when growth and decay are in equilibrium; but with the reservations that this point — and the length of the cycle — appear to differ on different sites, and that the total age of the stand may also influence biomass. Finally, it is tentatively concluded (within the limitations outlined above) that the rate of basal area growth, in terms either of area or of the individual tiller, is the most satisfactory of the characters studied here for use in comparisons. More precisely, the basal area per unit area of the largest tillers, since total basal area may depend, up to a point, on stand density. To reduce the effect of environmental gradients, such comparisons should preferably be made on material from the closed stand.

Much, however, remains undone. It remains to discover the origin of some of the differences between stands and within stands, such as in leaf : shoot ratios and in particular, the relationship of mineral nutrient content with age. Most of these problems have been discussed here; both experiment in controlled environment, and field observation, together with a suitable experimental design, will be necessary if these problems are to be further investigated. The limited compass of the present material must be extended if generally applicable results are to be obtained.

Conclusions

The bilberry stand consists of individual, branched rhizome systems the age of which increases towards their proximal end. Living tillers are found on the distal half of each rhizome unit, the oldest being near the middle of the unit. Assemblages of these units form the stand.

Growth is primarily centrifugal but later becomes increasingly complex. The rhizome units form successive generations, disposed in such a way that the older tillers of one accompany the younger of the unit immediately behind it. The complex, uneven-aged hierarchy of tillers is a result of this.

Each rhizome generation is derived from its predecessor by separation as a lateral branch from the older rhizome, by decay, insect larval activity or both. The length of each rhizome is limited by the growth of the distal end and the decay of the older proximal end.

Bilberry stands having such a structure are clones. All stages in the development of the stand can be seen, the earliest stages having generally unbroken rhizome connections and typically, a small area. The area of a stand is linearly related to its age, since the rate of rhizome growth appears to be constant. It is probable that the large communities in which bilberry dominates are aggregates of these clonal stands.

Each rhizome unit—by extension, each generation—represents a sequence in time, its length being equivalent to a period of ca 30 years. The tillers attain an age which on the Hamra and Garpenberg sites was about half that of the rhizome; the position of Cammachmore in this respect is obscure, since the oldest tiller was 34 years old, and the rhizome was not examined. Longevity is considered to be characteristic of a site.

The age structure of the stand primarily determined a large part of the spatial variation in standing crop, production of leaf and shoot, progression of basal area and probably performance. Distribution of fruits was also related to the age structure. The environment in the peripheral and inner parts of the stand modified the expression of age, but was not studied in detail.

Total biomass in the Garpenberg stands reached a maximum between the twelfth and fourteenth year and was greater than that at Hamra. At Hamra, maximum biomass was attained somewhat earlier than was the case at Garpenberg: there were, however, considerable differences within each site.

In G/IV (1967) the leaf content of N, P and K, the shoot content of N, P, K and possibly Mg were higher than those at H/II (1967). Similar indications were found for shoots (all elements studied) in G/IV (1966) and H/III (1967). No relationship could be demonstrated between mineral nutrient content of leaf or current shoot, and age, on the basis of samples of quadrat populations. Because of shortcomings in sampling procedure and the small number of samples, these conclusions are tentative. The large spatial variations in leaf and shoot contents of most elements studied remain unexplained.

Leaf and shoot production varied widely, both within stands and between stands and sites, as well as years of sampling. Yield is, however, related to the age of the system at any point. The differences between stands in leaf : shoot ratios, and between years, require further study.

Of the characters studied here, accretionary characters, such as standing crop, biomass and basal area of the largest stems, were most clearly related to age and provided the most satisfactory means of ranking stands. It is considered most appropriate to compare stands in respect of biomass at the age at which growth and decay are in equilibrium. This point probably differed between the sites studied, and the total age of the stand may also be a source of variation in biomass.

Basal area increment is considered to be the most useful character for comparison, either in areal or individual terms. The basal area of the five largest stems is probably a more suitable character for comparison than total basal area, since the latter is partly dependent on stand density.

It would be of advantage to test clonal material under controlled conditions, partly to assess the effect of environment on some of the growth characters used here, and partly to place comparisons on a firmer basis.

Summary

This investigation was concerned with the age structure and dynamic relationships in isolated bilberry (*Vaccinium myrtillus* L.) stands, mainly on two forest site types in Middle Sweden.

The stands were investigated by means of transects of contiguous quadrats or interrupted transects, which passed through the stand at right-angles to its advancing edge. Quadrats 25 x 25 cm, selected on the basis of the morphological scale of the plant, were used for sampling. All tillers arising within the quadrat were harvested and all rhizomes under it were excavated. This material was dried to constant weight at 105°C and separated as follows: aerial shoots into leaf, current long and current short shoots, and older shoots; in some cases C+1 shoots were also separated, and the number and weight of fruits present was recorded. All fractions were weighed. The individual and total length of all current long shoots was measured. On the five stems on each quadrat with the largest basal diameter over bark, annual rings were counted on basal TS and diameter under and over bark was measured under the microscope. Leaves and current shoots were reserved for mineral nutrient analysis, the latter also for determinations of weight : length relationships.

The rhizome was separated into three classes of diameter over bark, each class being weighed separately. Samples were taken from the two largest diameter classes for sectioning, age determination and diameter measurement. The total length of rhizome in each class was also measured. The thickness of the humus and litter layer was measured on each quadrat.

At a site Cammachmore, in eastern Scotland, samples were taken from an unusually luxuriant, long undisturbed stand of bilberry for population analysis. The age of all stems was determined and their diameter over and under bark measured as above. In addition, the width of the annual rings was measured with the aid of a projecting microscope. No further material was collected from this site at the time.

At Garpenberg and Skogshögskolan (Stockholm) in Sweden rhizome systems were excavated and mapped. The age of tillers and rhizomes was determined as far as feasible.

The results show that bilberry stands expand centrifugally by rhizome growth to form a large, expanded plant. Rhizomes branch in such a way that the primary rhizome is overlapped for most of its length by later branches. From the distal end of the rhizome tillers arise; as the age of the rhizome increases from the distal to the proximal end, so also does that of the tillers. The living tillers occupy approximately half of the rhizome's length. The overlap of rhizomes results in a complex age structure amongst the tillers, there being a few large, old tillers and numerous younger, smaller ones. This tiller age structure is a constant

feature throughout the population of a stand. Stand density increases from the outer to the inner part of the stand, by a process of "filling in" by the growth of tillers from rhizome branches, lateral rhizome buds and basal buds.

The standing crop aboveground follows a pattern related to the age structure of the rhizome; standing crop and the basal area of the five largest stems on each quadrat are correlated with the age of the oldest tiller on the quadrat. Leaf and current shoot weight are similarly related to age.

Rhizome weight and length increase into the stand, the weight of the large rhizome attaining a maximum close to the generally decayed end of the rhizome. The maximum standing crop of rhizome is attained at an age of ca 20 years, that of the aerial shoots at an age of ca 12 years, somewhat earlier on the site at Hamra (south of Stockholm). Total biomass is greatest at rhizome age ca 14 years for the Garpenberg material, earlier at Hamra.

Stands expand at a rate of ca 7 cm per annum radially, although the rate of rhizome growth in length may be considerably greater. The maximum age attained by the aerial shoots was 15 years at Garpenberg and ten years at Hamra; however, a 34 year old tiller was found at Cammachmore, and was still vigorous. The maximum age attained by the rhizome was ca 28 years at Garpenberg and ca 23 years at Hamra. Rhizome was not studied at Cammachmore.

The tiller populations studied consisted of the five largest stems at Hamra and Garpenberg, plus a subsample from Garpenberg IV, and of all tillers on two quadrats at Cammachmore. The age structure and diameter class distribution of the populations were similar, although the older populations tended to become progressively more positively skewed. Standing dead tillers at Garpenberg made up about five per cent of all tillers, but increased to ca 17 per cent amongst the older tillers. There were no standing dead stems amongst the five largest stems at Hamra. At Cammachmore, dead tillers were concentrated to those less than seven years of age, and made up ca 18 per cent of the population. None of the older tillers was dead.

Stocking density was far greater at Cammachmore than at Hamra or Garpenberg, and the basal area of the five largest stems was also greater. Studies of basal area growth rate indicated that tillers grew at a rate similar to that of the Hamra and Garpenberg tillers in the earlier years at Cammachmore, but that by the eighth year their basal area was greater and continued to increase when those at both Hamra and Garpenberg had declined. This evidence suggests that competition in the denser stand at Cammachmore may be severe in the early stages.

There is some evidence that the populations at Cammachmore had reached carrying capacity, although this (as expressed in terms of total basal area) may be characteristic of a site. In such a situation, ingrowth into a stand and survival may be determined by the death of a senior tiller.

In the youngest age classes at Cammachmore, there were more tillers than in the older. The average annual ingrowth, as calculated by dividing the total number of tillers alive at sampling by the length of the period between ingrowth and maximum age, was approximately half the number of tillers present in the youngest (measurable) age classes. An attempt was made to estimate true ingrowth by applying a correction based on a calculated mortality rate of 0.57. This gave a figure for ingrowth closer to the observed, but should be tested on independent material from the same stand. There were, however, variations in the numbers of individuals in each age class which could not be satisfactorily explained. They may depend on ingrowth related to the death of a senior tiller, or on environmental variations.

Survivorship curves were drawn for all the populations studied, on the assumption that longevity and the age class distribution were adequately represented in the samples. The assumption of a constant mortality rate, inferred from the distribution of dead tillers in the Garpenberg populations, and used for calculating the ingrowth correction, was found not to be strictly correct, although deaths tended to occur with constant frequency once the youngest age classes were past. Half-lives were obtained for all populations, Cammachmore having the longest and Hamra III the shortest half-life. These population statistics depend on the correctness of the assumption that the age distribution in the samples represents that in the population at large.

The course of radial increment was studied in the Cammachmore material, in an attempt to elucidate relationships between ring width and growth. Other studies were made of the increase in weight of the angular aerial shoots with age, and of their relationship with ring width. The former study suggested that some of the more marked fluctuations in ring width were primarily endogenic, whereas others may have depended on external agencies: in this case, tentatively weather conditions. Further study is being made of this problem. Weight per unit length, hence diameter, of the aerial shoots increases with age. After an initial period of long shoots, shoot length decreases with age, while the total number of shoots increases. Long shoots tend to give rise to relatively long shoots, and have numerous buds. Hence they develop a photosynthesising superstructure considerably greater than that developed on a shoot which was originally shorter. A consequence of this is that their subsequent diameter growth — increase in weight per unit length — is also greater, although it is probable that mechanical considerations are responsible to some extent.

Considering the bilberry bush as a system of axes which pass through this sequence, it is possible to construct an empirical model for growth. This might be used as a means of comparing weight increment on different sites, but requires further refinement. Vegetative shoots only are considered in the model, which in addition takes no account of losses.

The distribution of fruits and flowering shoots in the stand coincides with the distribution of the maxima for the longest shoots on each quadrat. Since leaf number, leaf size and shoot length are related, shoots on young axes having more and larger leaves than those on old, it follows that litter (consisting of leaf, fruit, flowers and some shoots) will

be greatest in those parts of the stand. No estimate has yet been made of the proportion of short shoots that fall as litter, since this depends in part on weather conditions — probably low temperatures in combination with thin snow cover — mainly during late winter.

The mineral nutrient content of leaves and current shoots was investigated in subsamples of the material. There was considerable spatial variation in most of the elements studied (N, P, K, Ca and Mg), which could not be demonstrated to be related to age. Owing to sampling shortcomings, differences between stands and years could not be reliably established. There were, however, indications that the leaf content of N, P and K, and the shoot content of N, P, K and possibly Mg in Garpenberg IV in 1967 was higher than that in Hamra II in the same year, and some confirmation of this was available for 1966 too. The origin of the spatial variation remains unexplained; further study should concentrate on analysis of tillers of known age at a clearly defined stage of development.

A comparison of the stands in respect of the characters studied indicated that accretionary characters such as standing crop and biomass as well as basal area of the five largest stems were most clearly related to age and provided the most satisfactory means of ranking stands. Over all, basal area increment in areal or individual terms is considered to be the most useful character for comparisons, and might for preference be based on the five largest stems on a quadrat, since total basal area is partly dependent on stand density.

REFERENCE MATERIAL

Appendix I

Methods

Age determination — stem counts

On the upper part of the bilberry axis, annual shoot increments are generally clearly defined. On the lower, cork formation and increasingly prostrate growth with age obscure them. Disregarding errors due to miscounts, there are three main sources of error in age determination by stem count-backs:

1. Death of axes. The bush is built up of a series of axes, the life-span of which is limited. Dead axes which have decayed are not available for counting, and truncated axes give unreliable results. Failure to distinguish and count increments on the older axes will result in an underestimate of age. The error in age determination by this method may be said to increase with the age of the bush (cf. Fig. 1, Introduction).
2. Prolepsis. Some of the buds laid down in any year give rise to shoots in that year, long or short. Some of these fall as litter during the winter. Occasionally a further generation of shoots is produced on these proleptic shoots, but does not often persist. A more serious source of error is the growth of a long shoot from a terminal bud which fails to abort; such shoots tend to persist, and the branching point may be difficult to detect. Unusually long shoots must be examined carefully.
3. Delay in emergence. Orthotropic shoots may not emerge fully from the litter or moss layer (especially if this is luxuriant) for one to three growing seasons after initiation. See Fig. 2, 23. A stem count-back may underestimate age by up to three years, even in young tillers.

Growth phases

This method is analogous to that used by e.g. Watt in *Calluna*, and was employed by Zlobin (1961) in modified form. It has the advantage that bushes can be quickly classified by an observer familiar with the phases, but was not used in the present study. Age is of course only approximately assessed.

Ring counts

This method requires sectioning of the stem base and usually microscopic examination. A clearly identifiable character is required, in relation to which the stem base may be defined. The first adventitious root has been used in e.g. *Calluna*, but the position of this in bilberry is dependent on e.g. the luxuriance of the moss layer, and stems sectioned at this point will give an underestimate of age by up to five years. (In addition, rhizome weight is overestimated). Here the criterion used was the point at which there is a transition from ridged to smooth bark like that of the rhizome. Ideally, the point at which the orthotropic shoot

turns up should be taken as the shoot base, but this is not practicable in the field. Some error is therefore involved in age determination, but for practical purposes this may be insignificant.

Staining of TS is preferable. Phloroglucinol/HCl gives a rapid and vivid effect, but is objectionable because of the fumes and the risk of damage to instruments by corrosion. The method used here depends on the contrast at the boundary of two rings when an almost opaque, dark stain is introduced into the section, and on the retention of the stain in vessels. Ring boundaries are shown as a thin, black line. Staining is a purely physical, not a chemical, process. A mixture of ink (Permanent Black Quink), glycerol and water, 2 : 2 : 1 was used. Other types of ink were not tested. The glycerol slows down the drying out of the section, ca 30 μ thick. Microscopic examination at a magnification of ca X 60 - 100 on a binocular dissecting microscope enabled sections to be dealt with very quickly. (For wood anatomy, see Mork 1946 b).

Rings are irregular and may be incomplete. Therefore, several radii should be examined, and preferably at least two sections of each stem. In old stems which are eccentric, rings were counted and compared on the two or three greatest radii; there is obviously a subjective element in ageing stems by ring counts. As a check on accuracy, serial sections were made on the aerial shoots of 25 bushes of various ages, through each annual shoot increment to the current shoots. In young axes (less than ca eight years old), increments of shoot were in agreement with the number of rings at the base. In older shoots, the difference in the two age estimates widened, shoot count-backs persistently underestimating age.

There are two main sources of error: First, that ring width tends to decrease down the axis, although somewhat irregularly. Thus basal rings may be so narrow (less than ca 0.005 mm) that even when the projecting microscope is used, the ring may not be counted. Secondly, the current year's ring may not be fully formed at the time of sampling in autumn, and may not be counted. The risk of error increases with the age of the bush, but up to 15 years of age is likely to involve an underestimate of age by one year at most. In older bushes underestimates of at least two years might be expected.

For rhizomes, the procedure is identical, except that no check on the accuracy of ring counts in old rhizomes is possible. The main source of error is the influence of the proximity of a large root or aerial shoot on rhizome diameter. Extra rings may be formed; by contrast, the attenuated rhizomes between such expansions may have fewer rings than expected from their position. Except where branching takes place, the boundary between annual rhizome increments is indistinct, but the age of primary branches generally agrees well with that of the parent rhizome. Ring boundaries are less clearly defined in rhizome than in the aerial shoots, and older rhizomes are almost invariably eccentric, with their largest radius downwards. Rings were counted mainly on this part of the section. Underestimates of ca two years might be expected in the older rhizomes, but no method of checking ages has yet been discovered.

Ring width was measured on a calibrated projecting microscope, complete traces being made for all sections. Ring width was then measured on the trace with a rule divided into half-millimetre units, several radii being measured. The screen scale was 72.5 units to the millimetre; the error of measurement on the tracing was ca 0.25 mm. For very narrow rings, therefore, the error of measurement was approximately equivalent to the width of the ring. A greater magnification would remove this measurement error, but would simultaneously introduce errors of distortion and overlap, besides reducing the distinctness of contrast between rings.

Bark thickness was measured on the ridges.

Rhizome was separated into diameter classes by means of a V-shaped wedge. The limits were as follows :

Small rhizome, less than 1.5 mm diameter over bark,
 Medium rhizome, 1.5 - 2.5 mm over bark,
 Large rhizome, more than 2.5 mm over bark.

Each length of rhizome was gauged at the ends and in the middle, avoiding expansions. The method is approximate, but quick and easy to use. The diameter limits refer to the dry rhizome; "wet" diameter, i.e. that measured under the microscope, seems to correspond approximately to live diameter.

Weight : length in shoots

Shoots used for the study of weight : length relationships were dried at 105°C, allowed to cool in a desiccator and weighed without delay. Their length was then measured to the nearest millimetre. Some of the older shoots were sectioned as a check on age.

Mineral nutrient analysis

Samples were dried to constant weight at 105°C. Those intended for analysis were ground and vacuum dried before weighing. Duplicate analyses were made of a solution in cases where analysis values diverged more than usual.

Nitrogen was determined by the micro-Kjeldahl method, using Se instead of Cu catalyst.

Phosphorus was determined colorimetrically, according to Scheel.

Potassium was determined flame-photometrically.

Calcium was first precipitated as oxalate and centrifuged. The precipitate was dissolved in HCl and calcium was determined flame-photometrically.

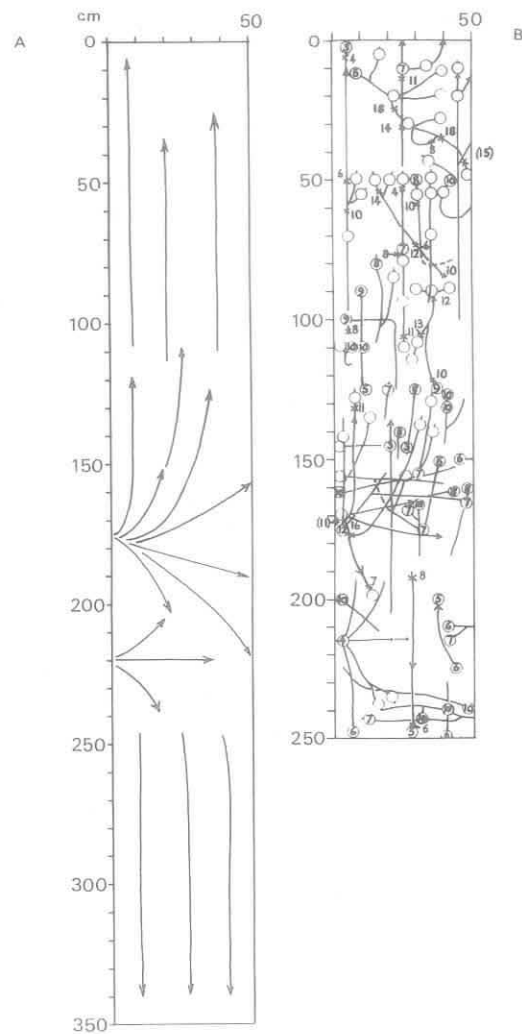
Magnesium was determined by the atomic-absorption method.

APPENDIX II

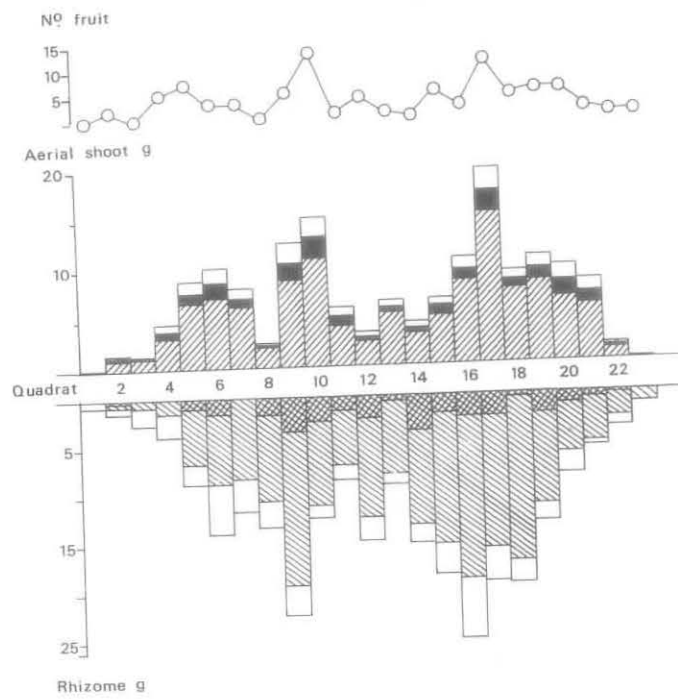
Site data

Stand No.	I	Garpenberg III	IV	Hamra II + III	Skogshögskolan	Cammachmore
Forest stand	spruce (d) pine (f) birch (o)	spruce (d) pine (o)	spruce (d) pine (r)	pine (d) understorey spruce (f)	oak (d) sparse sapling stand oak, cherry	birch, (d)
Vegetation	Grass-moss: D.flexuosa Pleuroz.schr. Hyloc.splen. Dicranum spp Ptilium c-c	Grass-moss: as G/I, plus Bryum sp & Melampyrum silvaticum (f)	Grass-moss: as G/I, plus Rhodobryum roseum in the interior	Cowberry-moss- lichen: (II) sparse lichen Calluna (r) (III) Cladonia spp (a) Cetraria isl.(o) Calluna (f) and re- mains of stems	mainly oak litter, some oak and cherry seedlings Anemone nem.rhiz- omes ubiquitous	mainly birch and bilberry litter Some Hyloc.splen. and Pleuroz.schr.
Geology & Soil	glacial till on leptite; sandy- silty, normally stony. Humus 10- 15 cm, charcoal abundant. Above highest coastline (here ca 195 m)	as G/I : below HCL, till washed Mainly sand with some gravel, much charcoal (old char- coal pit). Humus 10- 15 cm, lower bound- ary indistinct	as G/I but HCL, till washed below HCL More gravel	glacifluvial eskar : coarse, gravelly sand, very stony Humus 5-10 cm, indurated	Stockholm granite: thin layer medium sand with incorpor- ated humous mater- ial over bedrock	Precambrian gneiss overlaid by till from O.R.S.conglomerate. Coarse, sandy till, 10-20 % clay, many stones and boulders. Ca 30 cm peat, with old <u>Eriophorum</u> tus- socks
Hydrology	Well drained	Well drained	Well drained	Excessively drained, liable to drought	Well drained	Drainage impeded
History	Estate map of 1855-57 shows un- enclosed forest. Probably grazed (Forest stand felled 1966/67)	Roadside site: probably grazed in past. (Felled 1966/67)	As G/III	Forest stand self- sown after forest fire, now ca 60 years old	Enclosed park for ca 60 years	Relict wet heath, sur- rounded by agricultural land. Not grazed or bur- ned since ca 1928, and possibly not since 1860
		Note (1), (2)		Note (3)		Note (4)

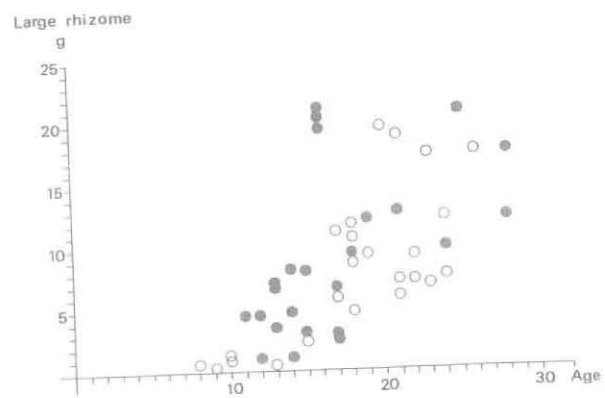
Notes: (1) Samuelsson (1960) (2) Troedsson (1956) (3) Holmen & Nömmik (1967) (4) Barclay-Estrup (1966)



Appdx Fig. 1. (A) Schematic representation of rhizome growth direction in a strip 50 x 350 cm at right-angles to the long axis of a bilberry stand (G/I). Excavated entire, dissected in laboratory. (B) shows the position and age of tillers and rhizomes in part of the strip, also somewhat schematised. Open circles—unaged tillers, crosses—rhizome section points. Numerous rhizomes were broken or severed during excavation. Compare Fig. 3, 4, 5.

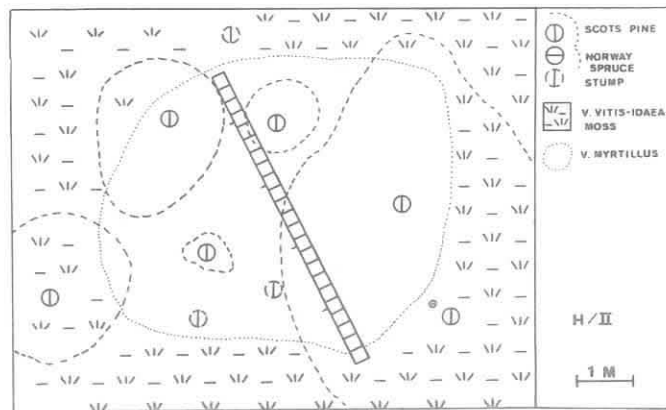
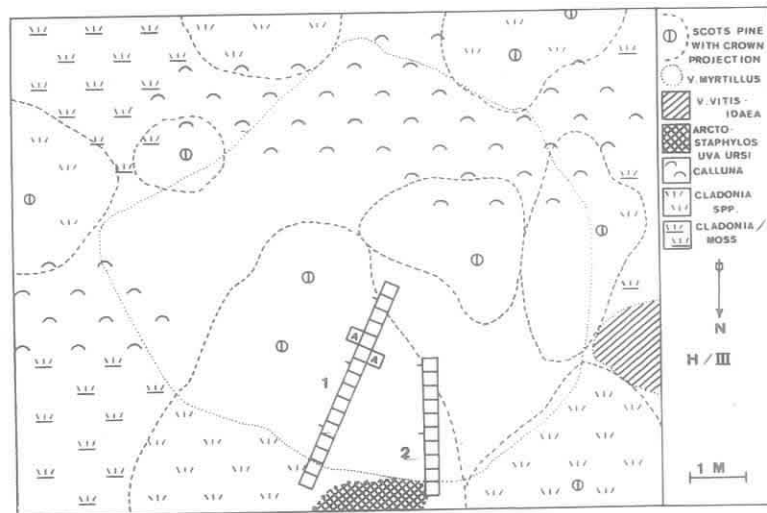


Appdx Fig. 2. Aerial and rhizome standing crop, H/II.



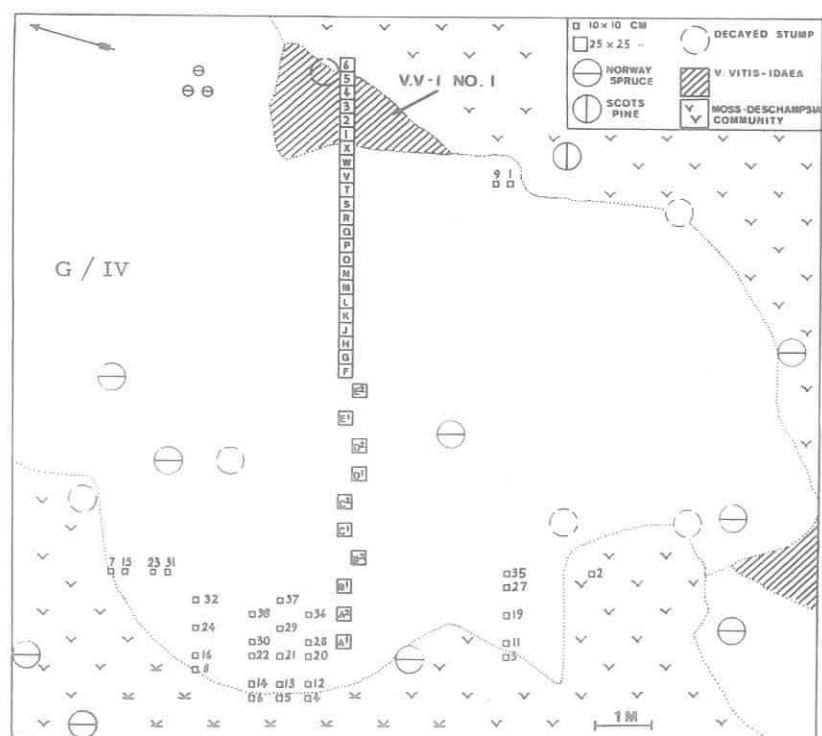
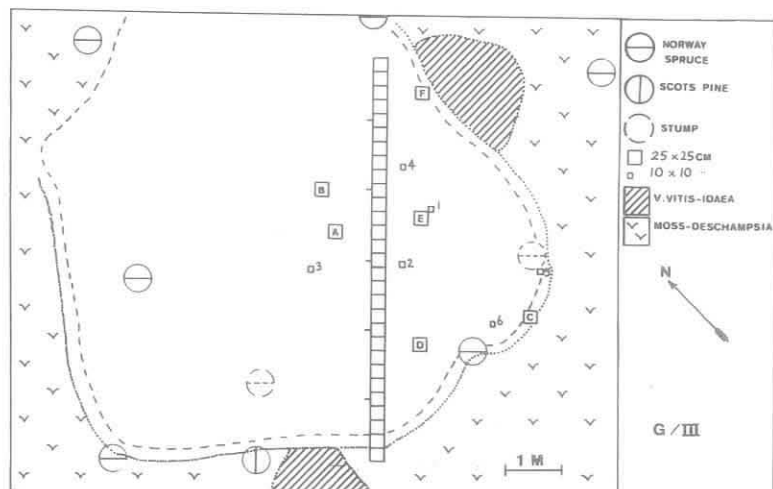
Appdx Fig. 3. Weight of large rhizome on age, cf. Fig. 16.

Appdx Fig. 4. Sampling layout in H/III.

Appdx
III

Appdx Fig. 5. Sampling layout in H/II.

Appdx Fig. 6. Sampling layout in G/III. The dashed line shows the boundary of the aerial stand, the dotted that of the rhizome.



Appdx Fig. 7. Sampling layout in G/IV.

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Sammanfattning

Sambandet mellan åldersfördelning och observerade variationer inom beståndet vad avser biomassa, blad-, skott- och bärmängd, undersöktes hos isolerade bestånd av blåbärsris, främst på två ståndorter i mellersta Sverige (Garpenberg och Hamra). Rispopulationens struktur och dynamik undersöktes även vid Cammachmore i östra Skottland.

För bestämning av biomassa och produktion per ytenhet, undersöktes bestånden dels genom att risets jordstammar grävdes fram, dels med hjälp av provrutor (25 x 25 cm) utlagda i bält (Bilaga III, fig. 4-7). Provrutans storlek anpassades till blåbärsrisets morfologi (jfr s. 3).

Biomassans, blad- och skottmängdens fördelning inom beståndet sammanfaller med åldersföljden, såväl ovan som under markytan, jfr fig. 8-9, 14-15 och 17. Sambanden mellan ålder och biomassa samt grundyta (BA₅, s. 23, 26) framgår av fig. 16, 19 och 22. Liknande samband finns mellan ålder och produktionen av blad och skott, jfr fig. 46-47.

Rispopulationen kan betraktas som en klonal hierarki, där ett fåtal gamla buskar bildar, tillsammans med yngre, ett starkt olikåldrigt bestånd (fig. 17, 26-30). Samspelet mellan antalet individer per ytenhet, grundyta samt mortalitet diskuteras. Under vissa antaganden jämförs populationernas "half-life" (fig. 31). Med samma antaganden skattas inväxningen, genom att korrigera för varje årsklass antalet individer vid provtagningsstillfället för avgång under ett viss tidsintervall, s. 43-44. Dock visar det sig, att antagandena ej gäller populationernas hela livslängd. Avgång under de första 2-3 åren kräver upprepade iakttagelser för att nöjaktigt kunna fastställas.

Individens tillväxt diskuteras i del 3. Typiskt för blåbärsriset är, att medellängden hos successiva skottgenerationer (E. current shoots) avtar, medan antalet ökar. Samtidigt ökar diametern hos äldre skott. Diametertillväxt kan uttryckas som en ökning i vikt per längdenhet, med hänsyn tagen till skillnader i diameter och tillväxt mellan skott av olika längd (fig. 32-37 och 45). På basis av dessa samband har en preliminär tillväxtmodell erhållits (fig. 43).

Förnafallets fördelning inom beståndet är starkt präglad av blåbärsrisets morfologi, d.v.s. åldersfördelning. Fig. 50 visar ett exempel på fördelningen av bär och skott inom ett bestånd (H/II), jfr även fig. 45-46.

Sambandet mellan ålder, och fördelningen av mineralnäringsämnen N, P, K, Ca och Mg inom beståndet diskuteras i del 4. Det visade sig, att provtagningsmetoden ej tillåter att något samband med säkerhet kan fastställas. Fig. 51-52 och tab. 13 visar att halten av vissa mineralnäringsämnen i blad och årets skott varierar starkt inom beståndet. Av tab. 14 framgår att skillnader föreligger mellan ståndorter. Dock

måste dessa samband undersökas vidare med förbättrad metodik, företrädesvis med utgångspunkt från åldersbestämda individer.

I del 5 jämförs olika sätt att uttrycka tillväxt och produktion hos blåbärsbestånd. Av de undersökta uttrycken för tillväxt, kan de som integrerar tillväxten under en följd av år, anses bäst lämpade, och av dessa, grundytetillväxten hos de fem grövsta stammarna (jfr fig. 18 och 53). Jämförs biomassan hos olika bestånd, borde jämförelsen gälla samma fas inom tillväxtförloppet (fig. 54).

Slutligen diskuteras problem som återstår eller som uppkommit. En mera experimentell inriktning, jämte fortsatta observationer på ett större material, anses önskvärd.